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Review of the Spirobolida on Madagascar, with descriptions of twelve new genera, including three genera of 'fire millipedes' (Diplopoda)

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Abstract

Twelve new genera and 37 new species of Spirobolida are described: *Corallobolus cruentus* **gen. n.**, **sp. n.**, *Sanguinobolus maculosus* **gen. n.**, **sp. n.**, *Colossobolus semicyclus* **gen. n.**, **sp. n.**, *C. oblongopedus* **sp. n.**, *C. giganteus* **sp. n.**, *C. minor* **sp. n.**, *C. litoralis* **sp. n.**, *C. aculeatus* **sp. n.**, *C. pseudoaculeatus* **sp. n.**, *Zehntnerobolus* **gen. n.**, *Flagellobolus pauliani* **gen. n.**, **sp. n.**, *Riotintobolus mandenensis* **gen. n.**, **sp. n.**, *R. minutus* **sp. n.**, *R. aridus* **sp. n.**, *R. anomalus* **sp. n.**, *Pseudocentrobolus aureus* **gen. n.**, **sp. n.**, *P. vohibasiensis* **sp. n.**, *Granitobolus endemicus* **gen. n.**, **sp. n.**, *G. andohahelensis* **sp. n.**, *Caprobolus andringitra* **gen. n.**, **sp. n.**, *Alluviobolus laticlavius* **gen. n.**, **sp. n.**, *A. tsimelahy* **sp. n.**, *A. antanosy* **sp. n.**, *Ostinobolus rufus* **gen. n.**, **sp. n.**, *O. stellaris* **sp. n.**, *O. montanus* **sp. n.**, *O. subterraneus* **sp. n.**, and *Hylekobolus brachiosauroides* **gen. n.**, **sp. n.**, *H. rufus* **sp. n.**, *H. griseus* **sp. n.**, *H. albicollaris* **sp. n.**, *H. goodmani* **sp. n.**, *H. montanus* **sp. n.**, *H. analavelona* **sp. n.**, *H. latifrons* **sp. n.**, *H. andasibensis* **sp. n.**, *H. marojejy* **sp. n.**, *H. anjanaharibe* **sp. n.** All genera and species are endemic to Madagascar. *Hylekobolus* belongs to the family Spirobolellidae, while all other Malagasy genera of Spirobolida belong to the Pachybolidae. Among them, only *Zehntnerobolus* **gen. n.** is based on a previously described species: *Spirobolus rubripes* de Saussure & Zehntner, 1897, whereas the remaining 11 new genera altogether contain (a total of) 37 new species. Three of the new genera are large-bodied "fire millipedes" (>100 mm long) with striking red/black colour patterns. The new discoveries increase the number of endemic Malagasy genera of Spirobolida more than fivefold (from 3

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to 15). The number of endemic species recorded from Madagascar has more than doubled (to 61). Body length of the new species varies greatly (between 23 and 170 mm). Keys to all Malagasy Spirobolida families, genera, as well as the newly described species, are provided. Four species, *Rhinocricus collaris* de Saussure & Zehntner, 1897, *Spirobolus grandidieri* de Saussure & Zehntner, 1897, *Spirobolus olympiaceus* Karsch, 1881, and *Spirobolus sikorae* de Saussure & Zehntner, 1897 are only known from females and are listed as *nomina dubia*. Some genera occur in the dry or spiny forest as well as in the rainforest ecosystem; species, however, are restricted to a single habitat type. In the rainforest, up to six different genera were collected in the same individual forest. Numerous genera are adapted to a special ecological niche. A high proportion of species are microendemic, often to some tiny, highly endangered forests. Of special conservation concern are the species which occur only in Analavelona, Ambatotsirongorongo, the subhumid, globally unique littoral forest of Petriky and the littoral rainforests of Mandena and Sainte Luce.

Keywords
Madagascar, biogeography, niche separation, endemism, Spirobolida, millipedes

Introduction

Madagascar, the third largest island in the world, harbours a globally unique fauna and flora (Lowry et al. 2001). The extraordinarily high number of endemic species, combined with the still ongoing habitat destruction (Green and Sussman 1990, Du Puy and Moat 2003), is the reason why Madagascar is listed as one of the world's ten most important biodiversity hotspots (Myers et al. 2000). The animals and plants from Madagascar are highly endemic and in many cases threatened with extinction. For example, all of Madagascar's large-bodied (>18 kg) land vertebrates are already extinct (Burney et al. 2003).

The large-bodied "fire millipedes" belong to the order Spirobolida and are among the most striking macro-invertebrates on the island. Fire millipedes are a heterogeneous (Wesener et al. 2008) assemblage of conspicuously coloured genera. The fire millipedes combine an unusually large body size (100–180 mm) with a singular blood-red/pitch-black colour pattern. Not surprisingly, the first endemic millipede genus to have been described from Madagascar was the fire millipede genus *Aphistogoniulus* Silvestri, 1897. A second Spirobolida genus, which also combines a black/red coloration with a large body size, *Madabolus* Wesener & Enghoff, 2008, has been described recently. *Madabolus*, however, is related to mainland counterparts, not to *Aphistogoniulus* (Wesener et al. 2008).

Three endemic genera of Spirobolida, *Aphistogoniulus* Silvestri, 1897 (see Wesener et al. 2009), *Spiromimus* de Saussure & Zehntner, 1901 (see Wesener & Enghoff, 2009) and *Madabolus* Wesener & Enghoff, 2008 (see Wesener et al. 2008) are currently known from Madagascar. In addition, two cosmopolitan, introduced species, *Leptogoniulus sorornus* (Butler, 1876) and *Trigoniulus corallinus* (Gervais, 1847) (see Shelley and Lehtinen 1999), as well as one widespread species of unknown origin (widespread near Zanzibar, in the Seychelles, on the Comoros and on Madagascar), *Dactylobolus bivirgatus* (Karsch, 1881) (see VandenSpiegel and Golovatch 2007), are

known from Madagascar (Enghoff 2003). New, large-scale inventories conducted by American museums all over Madagascar since 1990 accumulated a large number of millipede samples. These samples, along with some smaller museum collections and inventories conducted by TW in southeast Madagascar in the years 2003 and 2007 provided the basis for this study. Ecological data concerning Malagasy Spirobolida were also amassed for the first time.

While the giant pill-millipedes (order Sphaerotheriida) as well as the Chordeumatida from Madagascar are clearly related to their Indian counterparts (Mauriès 1994, Wesener and VandenSpiegel in press), the biogeographical relationships of the Spirobolida are still unknown. Surprisingly, only species of the suborder Trigoniulidea, with the single family Pachybolidae (excluding the dubious "*Rhinocricus collaris*") have hitherto been found in Madagascar (Enghoff 2003). Consequently at the family level, the fauna of Spirobolida is meagre in comparison to those from surrounding land masses. Even from the tiny Seychelles Islands, three families are known (Mauriès 1980, Golovatch and Korsós 1992).

Methods

Museum and collection acronyms:

BLF Collection code for Madagascar sample at CAS
CAS California Academy of Sciences, San Francisco, USA
CASENT Unique specimen codes of the entomology collection of the CAS
FMMC Millipede collection specimen code for samples at FMNH
FMNH Field Museum of Natural History, Chicago, USA
MNHN Muséum National d'Histoire Naturelle, Paris, France
ZFMK Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany
ZMH Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Germany
ZMUC Zoological Museum, University of Copenhagen, Denmark
ZSM Zoologische Staatssammlung München, Germany

Material: Museum specimens studied were from CAS (collected to 2007 by Brian Fisher, Charles Griswold and colleagues), FMNH (collected to 2003 by Steven Goodman) and MNHN, as well as material collected by K. Emberton in the 1990s and by Frank Glaw and Jörn Köhler in 2008. Additional material and ecological information came from field work by Jörg Ganzhorn, Kai Schütte (ZMH) and the senior author within a radius of about 50 km around Fort Dauphin (=Tolagnaro) in Southeastern Madagascar in February-March 2003 and May-July 2007.

Illustrations: Gonopods were drawn using a standard camera lucida. Mouthparts and antennae were studied in at least a single species of each genus using scanning electron microscopy (SEM). SEM samples were air dried directly from alcohol, sputter-coated for 240 seconds with gold and observed using a Zeiss (Leo) EVO SEM, based

at the FMNH. Other structures were photographed [multi-layer] using either a Microptics system based at the FMNH, or a Leica Z6 Imaging-System based at the ZFMK. All images were later modified using Adobe Photoshop version CS2 and assembled into plates using Adobe Illustrator version CS2.

Somatic versus gonopod characters: in Spirobolida, a similar habitus can be found in non-related taxa which live in the same ecological niche. In some cases, genera can only be distinguished by examining the gonopods (which are very distinct). Therefore, all new genera described in this study are characterized by similarities in the posterior and, to a lesser extent, anterior gonopods. Regardless of similarities or differences in the habitus, two species were assigned to the same genus only when unique similarities in the gonopods were detected.

Results

Order Spirobolida Cook, 1895

Key to the Malagasy families of Spirobolida

1 Posterior gonopods connected by a sclerotized sternite. Anterior gonopods without an apodeme, or only a small apodeme present; sternite never hyaline. Posterior gonopods usually complex. At least apical part of first basal joint of mandible visible (Fig. 1A) .... **suborder Trigoniulidea, single family Pachybolidae**

– Posterior gonopods connected only by membranous folds, sternite absent. Anterior gonopods with a well-developed apodeme, sternite hyaline but large. Posterior gonopods of long, slender, simple shape (Fig. 25O). First basal joint of mandible covered by collum (Fig. 27A), second basal joint forming a cavity for the short antenna (Fig. 25D). Part of head overlapping basal joints of mandible (Fig. 25D) ..... **suborder Spirobolidea, family Spirobolellidae**
On Madagascar only genus ***Hylekobolus***, **gen. n.**

Suborder Trigoniulidea: Family Pachybolidae

Suborder Trigoniulidea: single family Pachybolidae (Hoffman 1980). The elevation of the subfamily Trigoniulinae to family rank (Shelley 2003) is not followed here, since no character is known to discriminate between species of the Pachybolidae and Trigoniulinae.

Family Pachybolidae: unique characters are the posterior gonopods connected by a sclerotized sternite and the absence of long and slender apodemes on the telopodite and coxite of the anterior gonopod. The sternal apodemes are tiny or absent. The tracheal apodemes of the posterior gonopods are large, sometimes as large as the go-

nopod. Pachybolidae generally show a pantropical distribution in the Southern Hemisphere (Hoffman 1980, 1982).

Key to the Malagasy genera of Spirobolida of the family Pachybolidae:

1 Male coxa 5 with a process curved anteriorly and covering coxa 4 ..... ***Leptogoniulus* Silvestri, 1897**
only *L. sorornus* (Butler, 1876), introduced to Madagascar (Shelley and Lehtinen 1999).

– Male coxa 5 lacking processes, or if processes present, then never curved anteriorly. **2**

2 Anterior gonopod box-like, coxite and telopodite reaching similar height, lacking any processes. Collum unmodified. Preanal process absent..... ***Trigoniulus* Pocock, 1894**
Only *T. corallinus* (Gervais, 1847), introduced to Madagascar (Shelley and Lehtinen 1999).

– Anterior gonopods not box-like, or if box-shaped, then at least telopodite with a process, a well-developed preanal process and an enlarged collum (Fig. 31D)..... **3**

3 *Incisura lateralis* closed. Each *lamella lingualis* on gnathochilarium with four or more setae, all located at apical margin. Vulva kidney shaped, both valves meet in sinuous fissure ..... ***Madabolus* Wesener & Enghoff, 2008**
See Wesener et al. 2008

– *Incisura lateralis* open (Figs 1A, 13A). *Lamella lingualis* each with two setae located behind one another. Vulva simple, bivalve-like (Fig. 4)..... **4**

4 Adult males > 95 mm long and > 7 mm wide. Usually with blood-red/black colour pattern (Fig. 1A) **5**

– Adult males < 80 mm long and < 6.5 mm wide, colour never blood red/pitchblack..... **8**

5 Coxite of anterior gonopod with a slender, elongated process, longer than telopodite. Telopodite of posterior gonopod basally diverging into two slender branches, i.e. mesal main branch and lateral basal branch. Both branches curved towards one another, forming an 'O' or almost closed 'C'. Sperm canal always on mesal main branch .....***Aphistogoniulus* Silvestri, 1897** (ten species)
See Wesener et al. 2009

– Process of coxite of anterior gonopod short and wide, or, if slender, then never as long as telopodite. Telopodite of posterior gonopod not like above **6**

6 Telopodite of posterior gonopod large, with a blunt tip; branches or processes absent (Fig. 2C). Telopodite and coxite of equal length, fused, only suture visible (Fig. 1F). Telopodite of anterior gonopod with a large, triangular, retrorse process (Fig. 1E). Coxite with a slender, elongated process (Fig. 2A). Male tarsal pads present only to midbody legs..... ***Corallobolus* gen. n.** (monotypic)

– Posterior gonopod always divided into at least two branches. Telopodite and coxite clearly separated by a suture and a membranous area. Often with a stout, finger-shaped mesal coxite branch at suture between coxite and telopodite (Fig. 6C). Coxite far longer than telopodite (Fig. 6C). Process of anterior gonopod telopodite never retrorse (Fig. 6B), process of coxite short and wide (Fig. 6A). Male tarsal pads present on legs 3 and beyond **7**

7 Telopodite process of anterior gonopod slender basally, proximally widely swollen (Fig. 6B). Telopodite of posterior gonopod is not divided into a lateral main branch and a mesal brance; no swollen area present (Fig. 6C). Sperm canal running through lateral branch (Fig. 6D)..... ..... ***Sanguinobolus*** **gen. n.** (monotypic)

– Telopodite process of anterior gonopod slender (Fig. 9D). Telopodite of posterior gonopod divided into a mesal main branch and a lateral branch (Fig. 9H). Membranous swollen area located between both branches (Fig. 9I). Sperm canal running through mesal branch (Fig. 9F) .... ***Colossobolus*** **gen. n.** (seven species)

8 Head with an antennal groove. Antenna protruding back to only body ring 2. Head sclerite overlapping part of basal joints of mandible (Fig. 25D). Mentum of gnathochilarium not subdivided by a suture (Fig. 25E) .... ***Dactylobolus*** **Golovatch & Korsós, 1992**

On Madagascar only *D. bivirgatus* (Karsch, 1881). Species occurs also on the Comoros, Seychelles and close to Zanzibar. Probably introduced (VandenSpiegel and Golovatch 2007)

– Antennal groove absent (Fig. 26C). Antenna at least protruding back to ring 3, often longer. Especially first basal joint of mandible swollen, projecting towards head, but never above ocelli (Fig. 26C). Mentum often subdivided by a suture (Fig. 26F)..... **9**

9 Sperm canal projecting above lateral margin of telopodite of posterior gonopod (Fig. 22G)..... ***Zehntnerobolus*** **gen. n.** (monotypic)

– Sperm canal never projecting above margins of telopodite of posterior gonopod, or, if so, then never at lateral, but at mesal margin **10**

10 Telopodite, coxite and sternite of anterior gonopod mesally noticeably elongated into slender processes. Mentum of gnathochilarium not subdivided ... . ***Spiromimus*** **de Saussure & Zehntner, 1901 (13 species)**

See Wesener and Enghoff, 2009

– Telopodite, coxite and sternite of anterior gonopod never altogether elongated into slender processes. Mentum of gnathochilarium basally subdivided (with two exceptions in *Riotintobolus*) by a suture (Fig. 26G)..... **11**

11 Telopodite of posterior gonopod strongly elongated into a simple flagellum (Fig. 23E). Telopodite of anterior gonopod not apically, but at mid-length (!) with a slender, retrorse process (Fig. 23D)***Flagellobolus*** **gen. n.** (monotypic)

– Telopodite of posterior gonopod never shaped like a simple flagellum. Telopodite of anterior gonopods never at mid-length with a slender, retrorse process **12**

12 Telopodite of posterior gonopod apically always with a flag-like membranous extension (Fig. 26M) ..... ***Riotintobolus* gen. n.** (four species)

– Posterior gonopod without a flag-like membranous extension..... **13**

13 Preanal process present, protruding (Fig. 26B). Collum greatly enlarged, ventrally longer than body ring 2 (Fig. 31A). Posterior margin of body rings with rectangular extensions (Fig. 33C). Rings moniliform, caudal margins uplifted (Fig. 31A) **14**

– Preanal process absent (Fig. 39C). Collum of usual shape (Fig. 39A). Body rings without extensions, not moniliform (Fig. 39C) **15**

14 Telopodite of posterior gonopods at mesal margin with a rounded disc carrying numerous small spines (Figs 31A, 34A, B), and a membranous process at mid-length (Fig. 34D) ..... ***Pseudocentrobolus* gen. n.** (two species)

– Telopodite of posterior gonopods without a disc, apically with a beak-shaped process (Fig. 37M), at mid-length without a process ..... ***Granitobolus* gen. n.** (two species)

15 Telopodite of anterior gonopod with a very long, thin, sabre-like process (Fig. 41B). Telopodite of posterior gonopod basally divided into two long, slender branches of similar length and width, resembling a U (Fig. 41D)..... ***Caprobolus* gen. n.** (monotypic)

– Anterior and posterior gonopods not shaped like above **16**

16 Process of anterior gonopod telopodite basally slender, apically wide and slightly swollen (Fig. 44E). Posterior gonopod without a swollen membranous area. Sperm canal discharging on lateral margin (Fig. 44H) ..... ***Alluviobolus* sp. n.** (three species)

– Anterior gonopod apically never with a slender process. Posterior telopodite apically with a swollen membranous area (Fig. 48J). Sperm canal discharging at mesal margin..... ***Ostinobolus* gen. n.** (four species)

***Corallobolus* Wesener, gen. n.**
urn:lsid:zoobank.org:act:BA629070-2487-4C2E-8330-C809079086DE

Type species: *Corallobolus cruentus* sp. n., monotypic

Diagnosis: distinguished from all other Malagasy spirobolidan genera by the following combination of characters: male tarsal pads present on legs of anterior body half only. Known specimens of *Corallobolus* possess fewer body rings than in any other known large-bodied Malagasy spirobolidan genus, 44–46 body rings only. Gonopods unique for large-bodied Spirobolida from Madagascar (Figs 1E, F): telopodite of posterior gonopod of unique shape, relatively large, simple and with a well-rounded,

blunt tip (Fig. 1F). Sperm canal running along mesal margin and discharging just below tip, area surrounded by short membranous folds (Fig. 2B). Shares a large body size (circa 100 mm) and aposematic red/black colour pattern (Fig. 1A) with *Aphistogoniulus* Silvestri, 1897, *Madabolus* Wesener & Enghoff, 2008, *Colossobolus* gen. n. and *Sanguinobolus* gen. n.. Preanal process sharp-edged as in some *Colossobolus* species, not extending beyond anal valves (Fig. 1B). Male coxae 3 and 4 without processes, similar to *Aphistogoniulus* species.

Distribution and ecology: only known from the montane rainforest in Andohahela (Fig. 5). Sympatric with *Aphistogoniulus* at Andohahela.

Etymology: *Corallobolus*, masculine, is composed of *corallinus*, coral-red, which refers to the blood-red colour pattern of the single constituent species, and *-bolus* a common suffix for genera in the order Spirobolida.

Corallobolus cruentus Wesener, sp. n.

urn:lsid:zoobank.org:act:C4059969-8D03-4116-8D94-BF7937CFDCA3

Material examined: 1 ♂, 1 ♀, *Holotype:* 1 ♂ (86 mm long), FMMC 5397, Province Toliara, RNI Andohahela Parcel 1, camp 3, montane rainforest, 1200 m, 24°35.0' S, 46°44.1' E, leg. S. Goodman, pitfall trap, 7–17.XI.1995. *Paratype:* 1 ♀, FMMC 5397, same data as holotype.

Description. *Measurements*: male holotype with 46 body rings, circa 86 mm long, 7.5 mm wide. Female paratype with 44 body rings, 103 mm long, 10.0 mm wide.

Coloration contrasting blood-red/black (Fig. 1A). Head, antennae, legs and entire telson red. Mesozonites on body rings completely black, metazonites laterally black, dorsally blood red (Fig. 1B).

Head: each eye (ocellarium) with circa 38 ocelli arranged in 6 or 7 vertical rows (Fig. 1A). Labrum with standard three irregular teeth and a single row of 10–12 stout marginal setae. Clypeus with two setiferous foveolae on each side. Antennal cavity present, not extending below eye. Antennae of medium length, protruding back to ring 4. Relative lengths of antennomeres: 1<2>3=4=5=6, antennomere 2 only slightly longer than others. Terminal antennomere with four large sensory cones located together inside a membranous area (Fig. 3A). Antennomere 5 latero-apically with five rows (Fig. 3B), antennomere 6 with one or two rows (Fig. 3A) of sensilla basiconica.

Gnathochilarium: of usual Spirobolida shape (Fig. 3C). Lamellae linguales each with two standard setae located behind one another. Stipites each with three apical setae. Hypopharyngeal crest with a field of spine-like structures. Central pads of endochilarium separated into two levels, group of 8–10 sensilla located apically in recessed area (Fig. 3D). Medial palps with one large group of sensilla each, located towards hypopharyngeal crest.

Mandible: external tooth simple, rounded; mesal tooth with three cusps (Fig. 3E). Five pectinate lamellae. Mesal margin of pectinate area with four or five rows of small slender spines. Molar plate with numerous (10–12) transverse furrows.

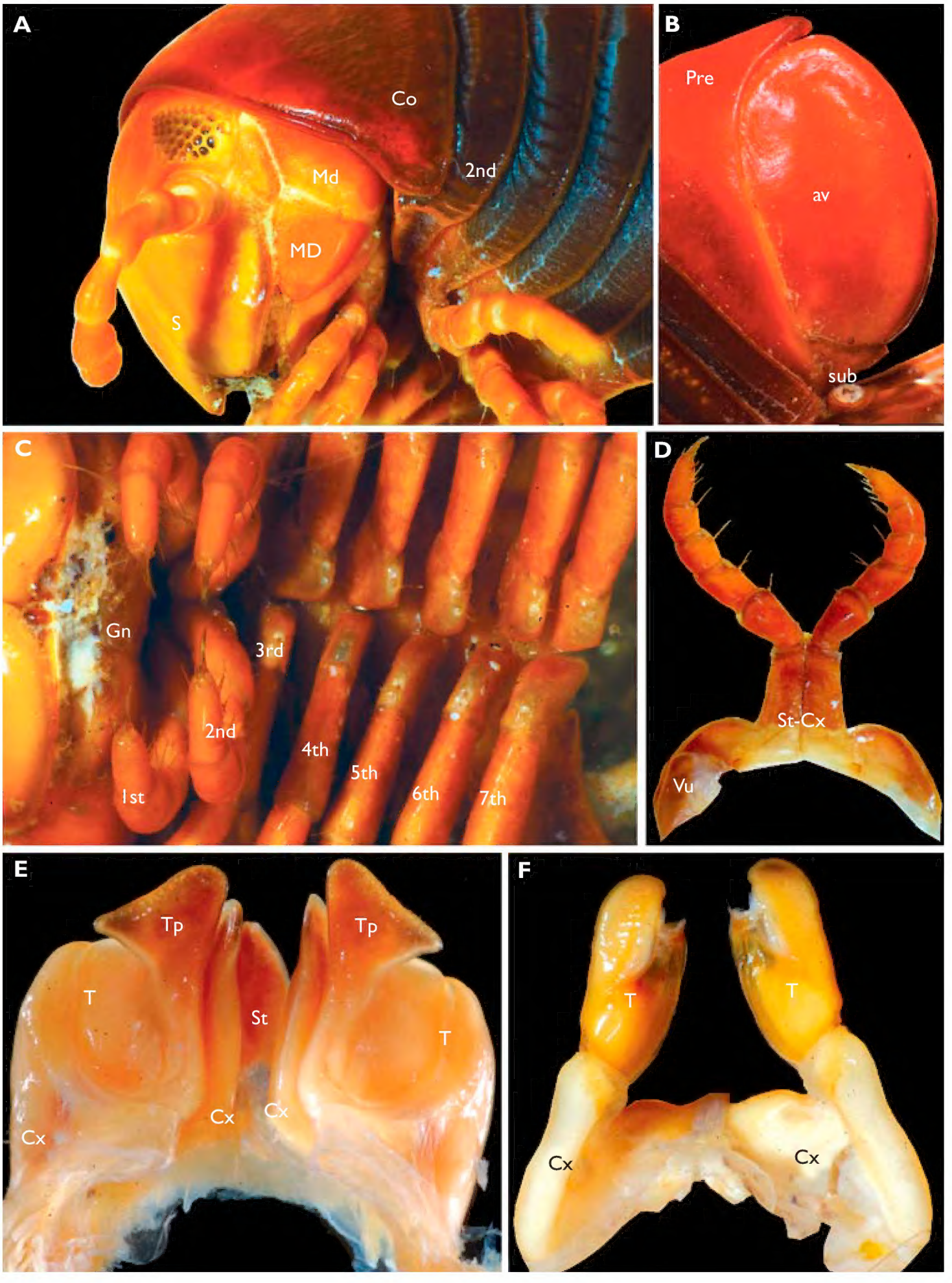


Figure 1. *Corallobolus cruentus* sp. n., A–C, E, F, male holotype, D female paratype. **A** head **B** telson **C** legs 1–7, ventral view **D** second leg pair with vulva, posterior view **E** anterior gonopods, posterior view **F** posterior gonopods, anterior view. av = anal valves; Co = collum; Cx = coxite; Gn = gnathochilarium; Md = basal joints of mandible; Pre = preanal ring; s = suture on clypeus; sub = subanal scale; St = sternite; T = telopodite; Tp = telopodite process; Vu = vulva. Not to same scale.

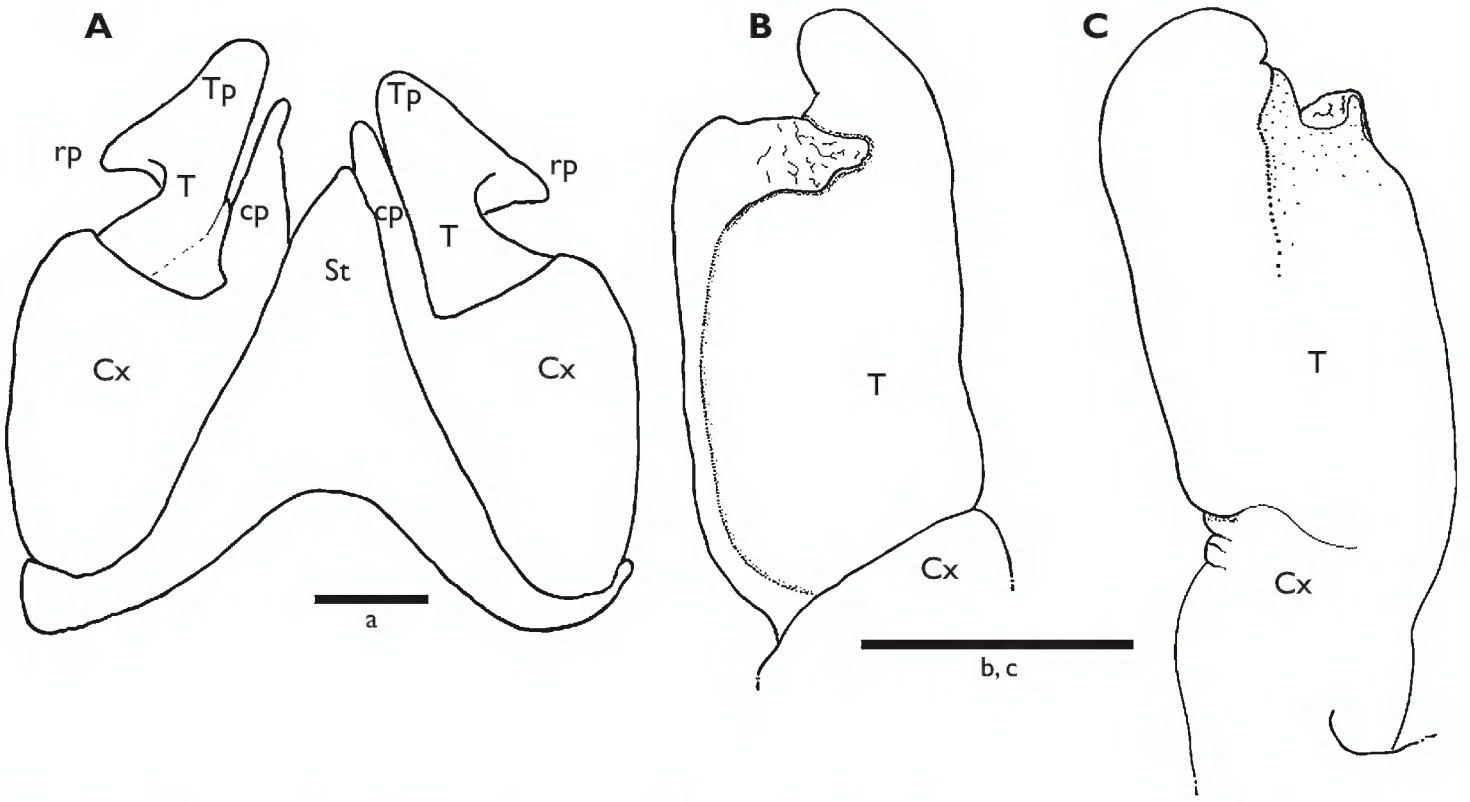


Figure 2. *Corallobolus cruentus* sp. n., male holotype. **A** anterior gonopods, anterior view **B** left posterior gonopod, posterior view **C** left posterior gonopod, anterior view. **Cx** coxite **cp** coxite process **rp** retrorse process **St** sternite **T** telopodite **Tp** telopodite process. Scale bars = 1 mm.

Collum: smooth, laterally not protruding as far as ring 2 (Fig. 1A).

Body rings: dorsally mostly smooth, on mesozona with some irregular punctation. Metazona and mesozona ventrally with longitudinal impressions. Ozopores starting at body ring 6, located in front of, but not touching suture between mesozona and metazona. Ozopore on ring 6 located much more ventrally than subsequent ozopores.

Telson: anal valves with well-developed lips and micropunctation but with neither grooves, nor setae. Preanal ring sharp-edged and slightly protruding, but not extending beyond anal valves. Subanal scale inconspicuous (Fig. 1C).

Legs: coxae 1 and 2 elongated and fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae (Fig. 1D). Length of midbody legs circa 1.3 times body diameter in males, circa 1.1 times body diameter in females. Each podomere with pair of apical, ventral setae. Coxae 3 and beyond of rectangular shape. Tarsus with a stout dorso-apical seta and a pair of stout ventro-apical ones in males, in females with three pairs of setae, of which apical pair stout, others successively much smaller.

Male sexual characters: tarsi 3 up to midbody legs with a tarsal pad not protruding past base of claw. Coxae 3–7 unmodified (Fig. 1B).

Anterior gonopod sternite elongated into a triangular process with a narrow tip (Fig. 2A). Mesal process of coxite slender and well-developed (Fig. 2A). Mesal process longer than sternite, but clearly shorter than telopodite. Telopodite with a large, wide, well-rounded process; retrorse projection large and well-rounded (Figs 1E, 2A).

Posterior gonopods unique (Figs 1F; 2B). Gonopod pair connected by a well-sclerotized sternite. Telopodites positioned parallel to one another (Fig. 1F). Coxite and telopodite in anterior view separated by a thin suture (Fig. 2C). Coxite simple, without

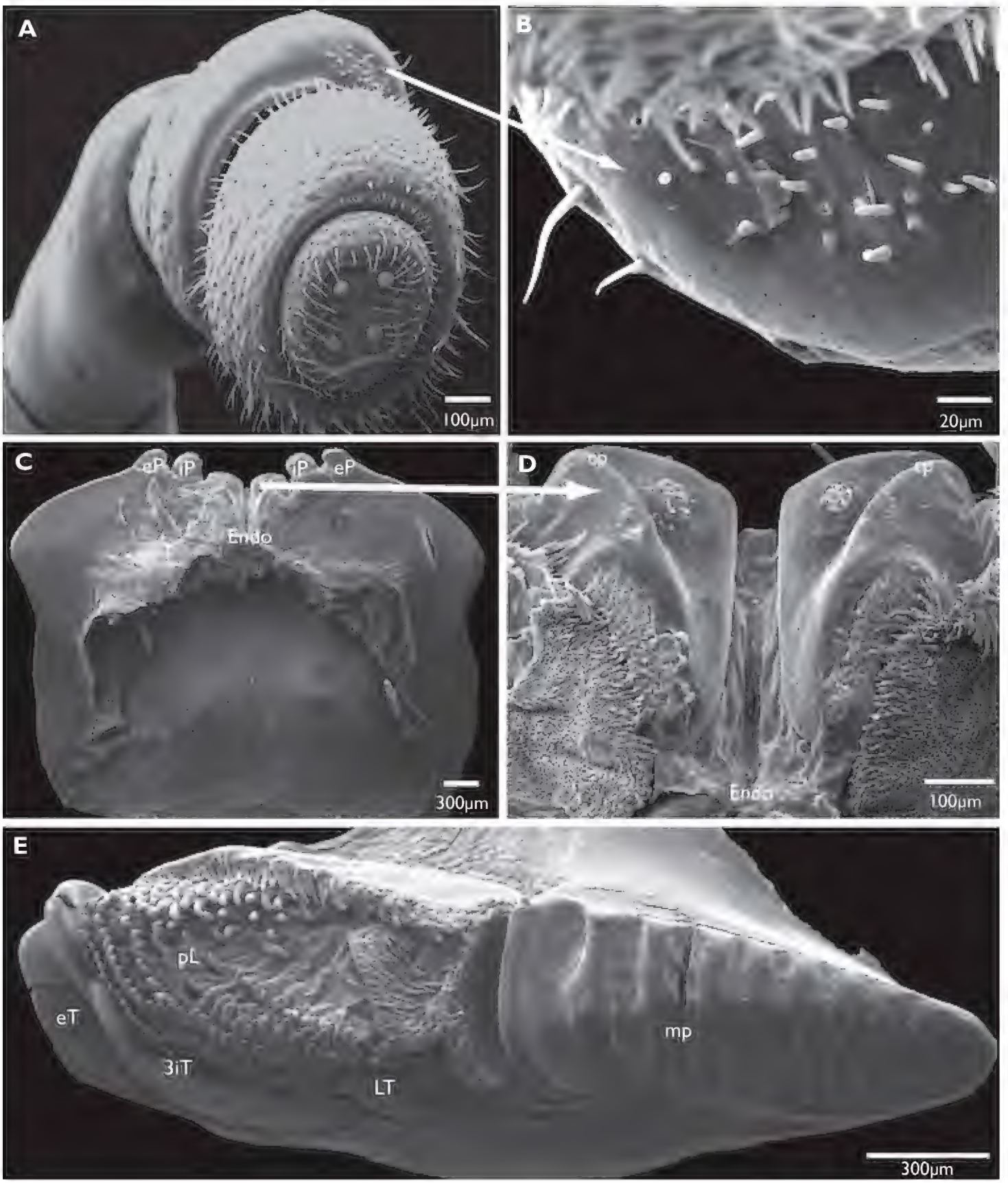


Figure 3. *Corallobolus cruentus* sp. n., female paratype, SEM **A** antenna, apical view **B** antennomere 5 with sensilla basiconica **C** gnathochilarium, dorsal view **D** endochilarium, detail **E** right mandible, mesal view. 3iT = 3-combed internal teeth; cp = central located pads, median palps; Endo = endochilarium; eP = external palpus; eT = external tooth; iP = inner palpus; LT = lateral tooth; Me = mentum; mp = molar plate; pL = pectinate lamella; St = stipites.

processes (Fig. 1F). Telopodite large, coaxial with coxite (Fig. 1F). Telopodite completely sclerotized, wide, well-rounded, without a sharp edge or a process (Figs 1F, 2B, C). Telopodite on anterior side at mesal margin with thin, membranous folds (Fig.

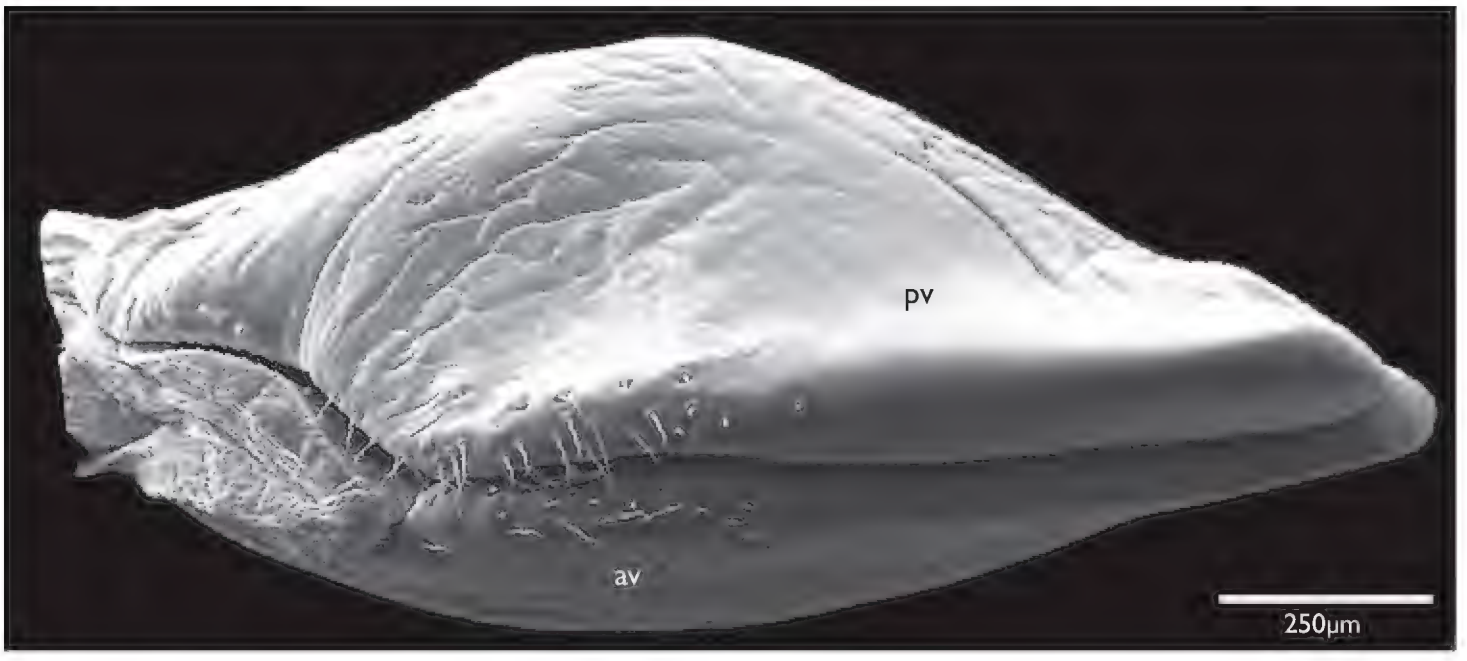


Figure 4. *Corallobolus cruentus* sp. n., female paratype, SEM, right vulva. **Abbreviations**: av = anterior valve; pv = posterior valve.

1B). Lateral margin protruding higher than mesal margin. Sperm canal running along mesal margin of gonopod and discharging into short membranous folds below tip of telopodite (Fig. 1F).

Female sexual characters: vulva simple, bivalve-like (Figs 1D, 4). Both plates basally with 2–3 rows of setae (Fig. 4).

Etymology: *cruentus*, adjective, refers to the blood-spotted colour pattern.

***Sanguinobolus* Wesener, gen. n.**
urn:lsid:zoobank.org:act:C699F031-ACE7-4624-8B68-4C153FAE59E1

Type species: *Sanguinobolus maculosus* sp. n., monotypic

Diagnosis: distinguished by male tarsal pads less prominently developed than in other large-bodied Malagasy genera of Spirobolida (Figs 7C, D), and by anterior telopodite process with a wide and apically swollen tip, unlike in any other Malagasy spirobolid genus (Figs 6A, B). Sperm canal on posterior gonopod discharging into membranous area of telopodite main branch (Fig. 6D). Shares a large body size (>100 mm) and an aposematic red-black colour pattern with *Aphistogoniulus* Silvestri, 1897, *Madabolus* Wesener & Enghoff, 2008, *Corallobolus* and *Colossobolus* gen. n.. Differs from *Aphistogoniulus* Silvestri, 1897 and *Colossobolus* gen. n. by the absence of a mesal branch on the posterior gonopod telopodite (Fig. 6C). The sperm canal in *Sanguinobolus* runs through the lateral branch, in *Aphistogoniulus* and *Colossobolus* gen. n. through the mesal branch. Differs from *Colossobolus* gen. n. in the absence of a central membranous area basally to the main branch of the posterior gonopod telopodite. *Sanguinobolus* resembles *Colossobolus* gen. n. in the presence of a short and wide mesal process on

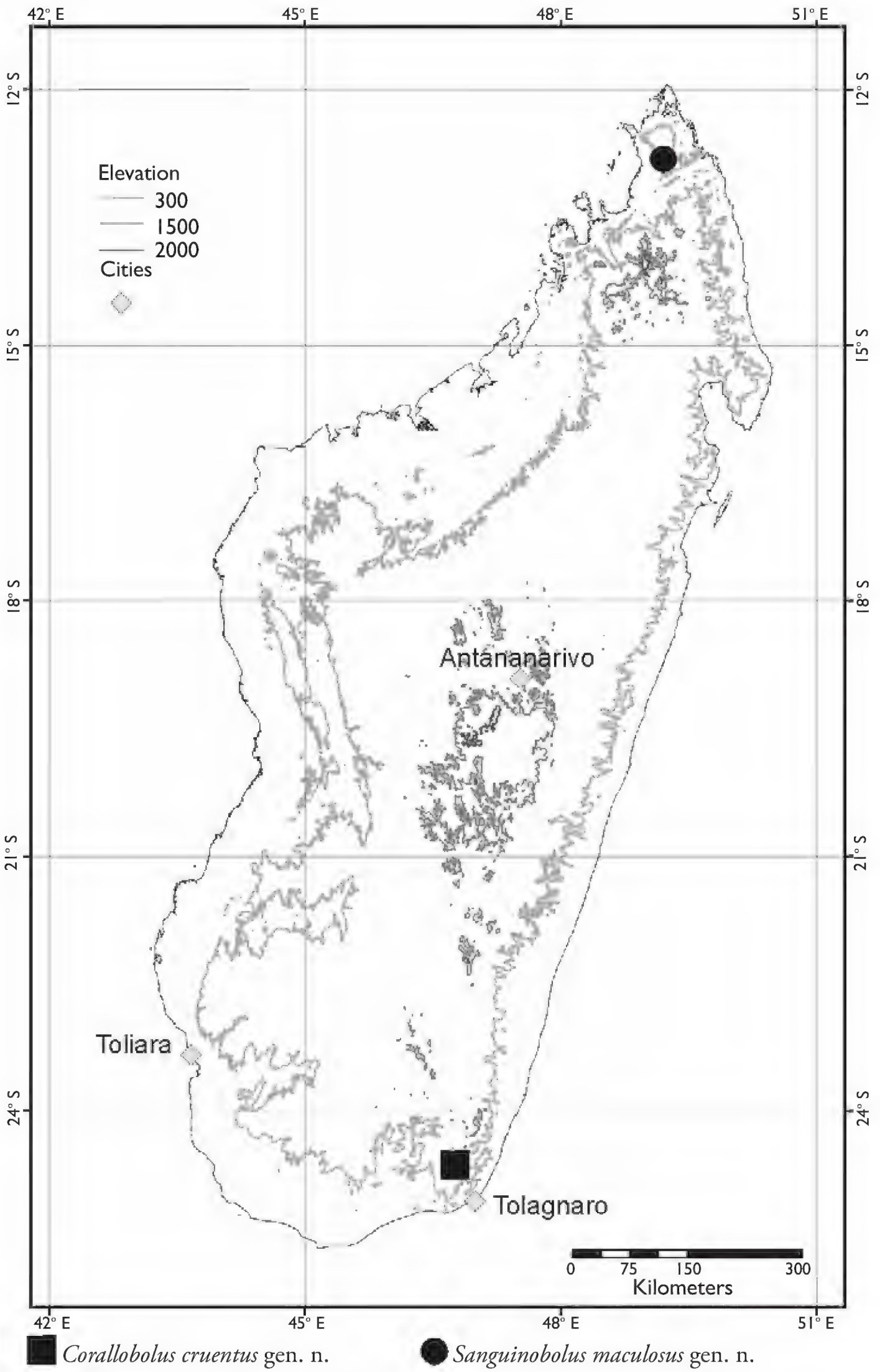


Figure 5. Distribution map for the genera *Corallobolus* gen. n. and *Sanguinobolus* gen. n.

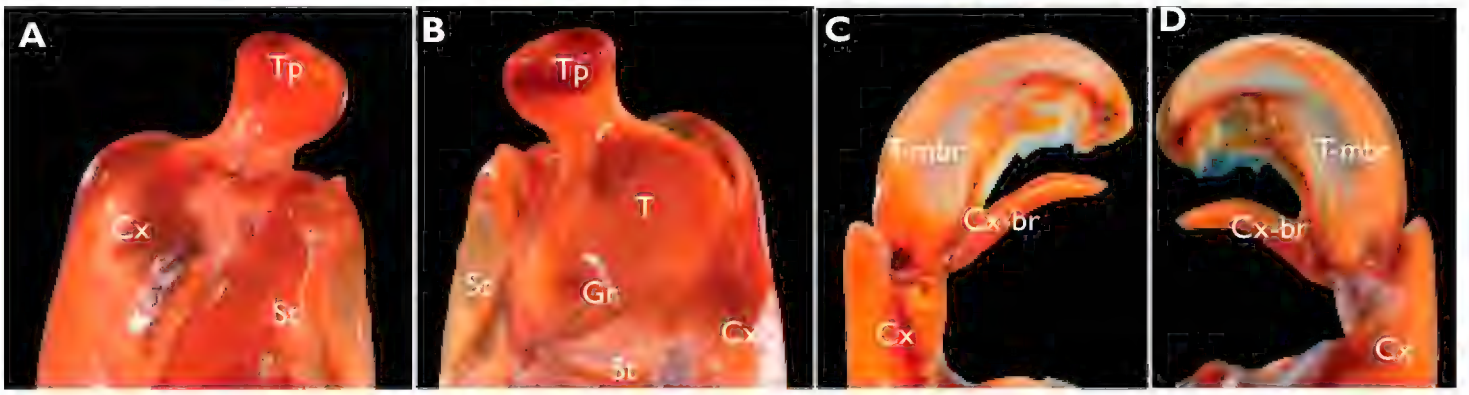


Figure 6. *Sanguinobolus maculosus* sp. n., male holotype. **A** left half of anterior gonopod, anterior view **B** left half, posterior view **C** left posterior gonopod, anterior view **D** left posterior gonopod, posterior view. Cx = coxite; Cx-br = coxite branch; Gr = groove on anterior gonopod; St = sternite; T = telopodite; T-mbr = telopodite main branch; Tp = telopodite process. Not to same scale.

the coxite of the anterior gonopod which is shorter or only slightly longer than the telopodite and sternite.

Distribution and ecology: only known from the isolated rainforest in Montagne d'Ambre, north Madagascar (Fig. 5). Species of the genus are probably active on the soil surface because of their relatively long legs and aposematic colour pattern.

Etymology: *Sanguinobolus*, masculine, is composed of *sanguinus*, blood, which refers to the blood-red colour pattern of the single constituent species, and *-bolus* a common suffix for genera of the order Spirobolida.

***Sanguinobolus maculosus* Wesener, sp. n.**
urn:lsid:zoobank.org:act:CD92BDAF-F533-40B5-A50B-DA179DE3B2CC

Material examined: 1 ♂, 1 F. *Holotype:* 1 ♂ (118 mm long), FMMC 3918. Madagascar, Province Antsiranana, Parc National Montagne d'Ambre, 3.6 km 235°SW Joffreville, 925 m, montane rainforest, 12°32'4" S, 049°10'46" E, leg. Fisher, Griswold et al., 20–26.I.2001. *Paratype:* 1 ♀, FMMC 3918, same data as holotype.

Description. *Measurements*: male holotype with 51 body rings, circa 118 mm long, 9.8 mm wide. Female paratype with 52 body rings, 120 mm long, 10.5 mm wide.

Coloration faded in alcohol. Head, antennae, legs and telson red. Body rings dirty red-brownish.

Head: each eye with circa 35–40 ocelli arranged in 7 or 8 vertical rows. Labrum with standard three irregular teeth and a single row of 10–12 stout marginal setae. Clypeus with two setiferous foveolae on each side. Antennal cavity present, not extending below eye. Antennae of medium length, protruding back to ring 4. Relative lengths of antennomeres: 1<2>3=4=5=6, antennomere 2 longest. Terminal antennomere with four large sensory cones located together inside a membranous area (Fig. 7A). Antennomere 5 latero-apically with four rows, antennomere 6 with three rows (Fig. 7B) of sensilla basiconica.

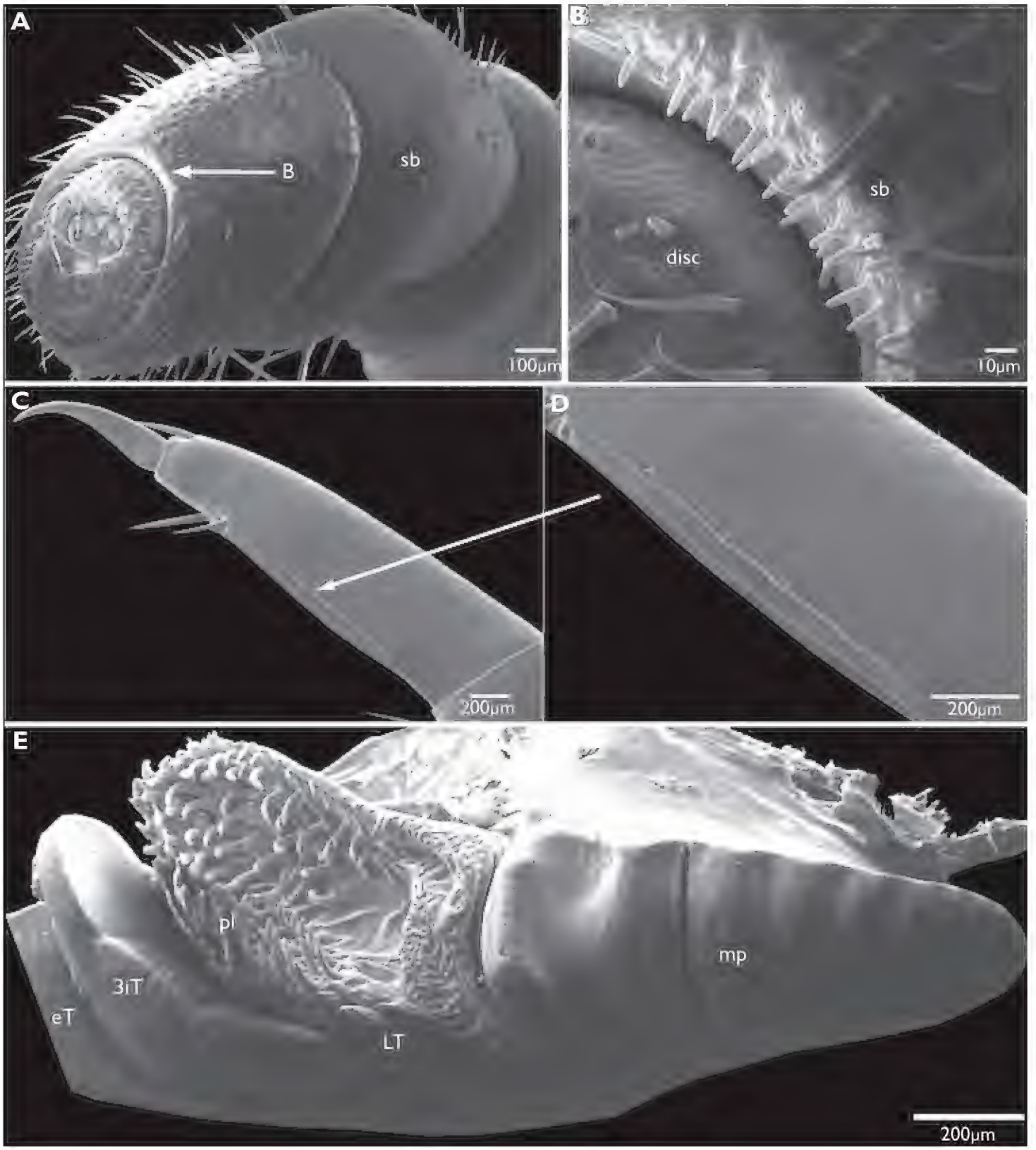


Figure 7. *Sanguinobolus maculosus* sp. n., male paratype, SEM. **A** antenna, apical view, arrow indicates area shown in 7B **B** antennomere 6 with sensilla basiconica **C** male left midbody leg **D** detail of tarsus **E** left mandible, mesal view. 3iT = 3-combed internal teeth; eT = external tooth; LT = lateral tooth; mp = molar plate; pL = pectinate lamella; sb = sensilla basiconica.

Gnathochilarium: of usual spirobolidan shape. Lamellae linguales each with two standard setae located behind one another. Stipites each with three apical setae. Palpi of gnathochilarium with numerous sensilla. Hypopharyngeal crest with a field of spine-like structures. Central pads of endochilarium separated into two levels, group of 10–12 sensilla located apically in recessed area. Medial palps with a large group of sensilla each, located towards hypopharyngeal crest.

Mandible: external tooth simple, rounded; mesal tooth with three cusps (Fig. 7E). Five or six pectinate lamellae. Mesal margin of pectinate area with circa two rows of small slender spines. Molar plate with numerous (8–10) transverse furrows.

Collum: smooth, laterally not protruding as far as ventral surface of body ring 2.

Body rings: mostly smooth, with some irregular punctation and some transverse impressions on mesozona. Metazona and mesozona ventrally with deep longitudinal impressions. Ozopores starting at body ring 6, located closely in front of, but not touching suture between mesozona and metazona. Ozopore on ring 6 located much more ventrally than subsequent ozopores.

Telson: anal valves with well-developed lips and micropunctation but with neither grooves nor setae. Preanal ring and subanal process well-rounded, not extending beyond anal valves. Preanal process inconspicuous.

Legs: coxae 1 and 2 elongated and fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae. Length of midbody legs circa 1.2 times body diameter in males, circa 1.0 times body diameter in females. Each podomere with an apical ventral seta. Coxae 3 and beyond of rectangular shape. Tarsus with a stout dorso-apical seta and a pair of stout ventro-apical ones in males, in females with three pairs of setae, of which apical pair stout, others successively smaller.

Male sexual characters: tarsi 3 and beyond with a small tarsal pad not protruding past base of claw. Mesal margin of tarsus towards tarsal pad carrying five grooves with short sensory setae (Figs 7C, D). An additional row of numerous short setae present on outer tarsal margin (Fig. 7D). Coxae 3 and 4 each with a short process protruding posteriorly, but never overlapping adjacent coxa.

Anterior gonopod sternite elongated into a wide, broadly-rounded lobe with a slightly narrowed tip (Fig. 6A). Mesal process of coxite weakly developed, protruding into a wide, very short process, shorter than sternite (Fig. 6A). Telopodite on posterior side basally with a circular groove (Fig. 6B). Telopodite process long, basally slender, proximally greatly enlarged into a characteristic swollen knob (Fig. 6B). Mesal margin not projecting (Fig. 6B).

Posterior gonopods unique (Figs 6C, D). Gonopod pair connected by a well-sclerotized and visible sternite. Telopodites positioned face-to-face with one another. Coxite and telopodite separated by a membranous area. Branch of coxite long and stout, almost as long as, but more slender than lateral main branch of telopodite (Figs 6C, D), latter curved towards opposite gonopod, not tapering (Fig. 6C). Main branch 2 times longer than wide, completely sclerotized. Mesal margin towards coxite branch with some membranous folds, which slightly protrude above mesal margin (Fig. 6D). Sperm canal discharging apically at mesal margin of lateral main branch.

Female sexual characters: vulva simple, consisting of two simple, subequally-sized, sclerotized plates, bivalve-like (Fig. 8). Both plates only basally with 3 or 4 rows of setae located towards opening. Anterior plate slightly larger than posterior one (Fig. 8).

Intraspecific variation: only known from holotype and a single female paratype.

Etymology: *maculosus*, adjective, refers to the spotted black-red colour pattern.

Figure 8. *Sanguinobolus maculosus* sp. n., female paratype, SEM, right vulva. **Abbreviations**: av = anterior valve; O = operculum; pv = posterior valve.

***Colossobolus* Wesener, gen. n.**
urn:lsid:zoobank.org:act:3F5F1E9A-F3BE-44F4-AB34-62DB25472FBD

Type species: *Colossobolus semicyclus* sp. n.

Other species included:
C. oblongopedus sp. n.
C. giganteus sp. n.
C. minor sp. n.
C. litoralis sp. n.
C. aculeatus sp. n.
C. pseudoaculeatus sp. n.

Diagnosis: distinguished by the slender telopodite process of anterior gonopods and the disc-like shape of posterior gonopod telopodite which is always divided into two branches. The sperm canal runs through the mesal branch and the area between both branches is basally membranous (Fig. 9F). Shares a large body size (90–170 mm) and an aposematic red/black colour pattern (Figs 9A, 13A) with *Aphistogoniulus* Silvestri, 1897, *Madabolus* Wesener & Enghoff, 2008, *Corallobolus* and *Sanguinobolus*. Male tarsal pads are prominently developed. Shares a wide and short coxite process of the anterior gonopods (Fig. 9D) with *Sanguinobolus*, while this process is slender in *Corallobolus* (Fig. 2A), and slender as well as longer than the telopodite in *Aphistogoniulus*.

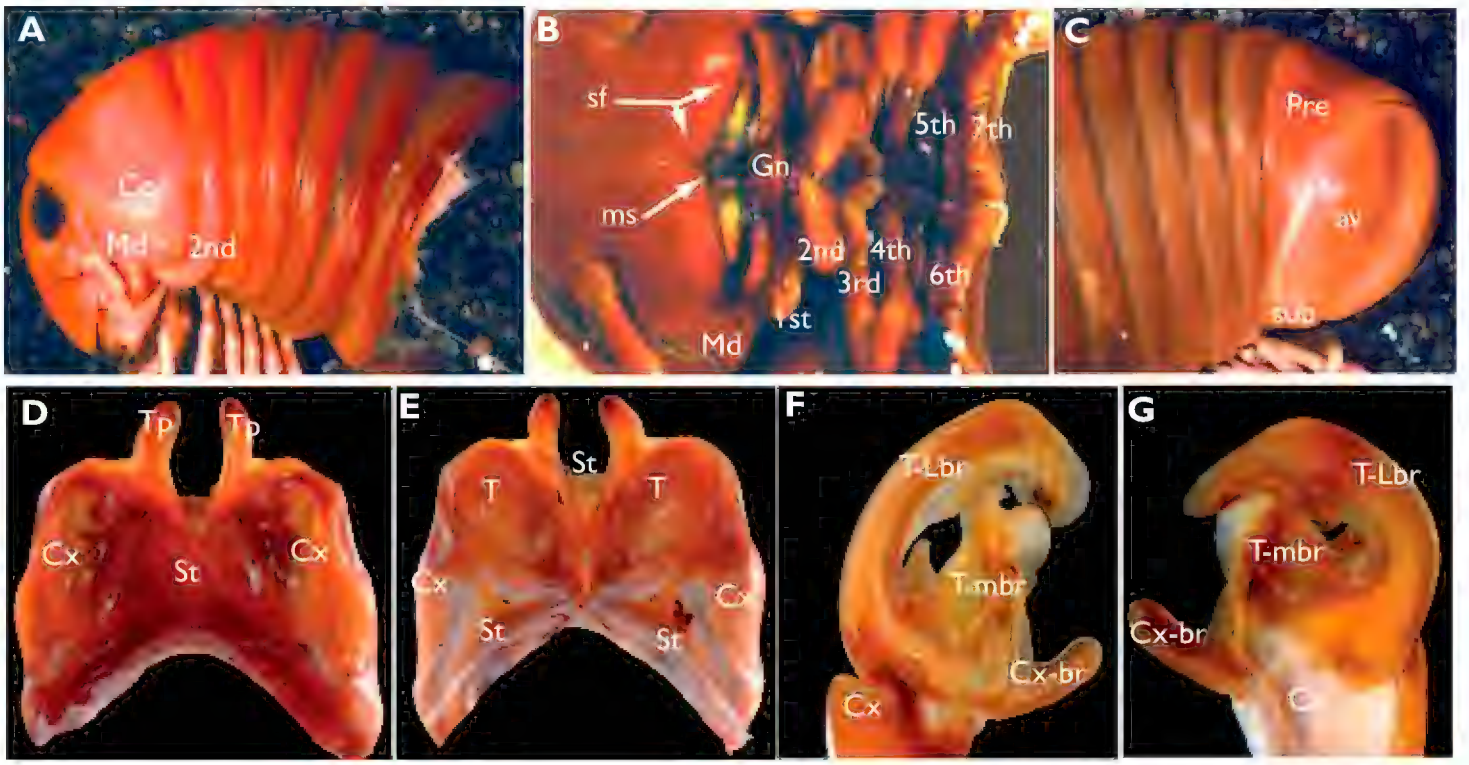


Figure 9. *Colossobolus semicyclus* sp. n., male holotype. **A** head **B** legs 1–7, ventral view **C** telson **D** anterior gonopod, anterior view **E** anterior gonopod, posterior view **F** left posterior gonopod, anterior view **G** left posterior gonopod, posterior view **H** posterior gonopod, anterior view **I** posterior gonopod, posterior view. av = anal valves; Co = collum; Cx = coxite; Cx-br = coxite branch; Gn = gnathochilarium; ma = membranous area; Md = mandible; ms = marginal setae; Pre = preanal ring; sf = setiferous foveolae; St = sternite; sub = subanal scale; T = telopodite; T-Lbr = telopodite lateral branch; T-mbr = telopodite main branch; Tp = telopodite process. Scale bars = 1 mm.

Distribution and ecology: species of *Colossobolus* have been recorded from littoral, dry and subhumid forests in northern Madagascar (Fig. 10). Two different *Colossobolus* species occur sympatrically at numerous sites, but no *Colossobolus* species have been found in rainforests. Species of *Colossobolus* and *Aphistogoniulus* occurred sympatrically on at least one site. Species of *Colossobolus* are probably active on the soil surface and might even climb trees because of their long legs, aposematic colour pattern and the fact that some species were caught in pitfall traps.

Description. *Males*: length up to 165 mm, diameter up to 12.0 mm, 47–52 rings. Females: length up to 128 mm, diameter up to 15.5 mm, 49–52 rings. Apodous rings absent in all adult specimens.

Coloration (after short time in alcohol): prozona and mesozona red or reddish-brown (faded to grey because of light or alcohol exposure in some specimens), metazona dark brown or black (Fig. 17). Ozopores surrounded in some specimens by a large black spot. Telson (also faded to grey in some specimens), head, antennae, gonopods and legs always red (Figs 9A, C).

Head: each eye with circa 35–40 ocelli arranged in 6–9 vertical rows (Fig. 9A). Labrum with circa three irregular teeth and one row of 10–12 stout marginal setae (Fig. 9B). Clypeus with two setiferous foveolae on each side (Fig. 9B). Antennal cavity present, not extending below eye (Fig. 13A). Antennae short, reaching back to ring 3 or 4 (Fig. 9A). Relative lengths of antennomeres: 1<<2>>3=4=5=6, antennomere 2 longest (Fig. 11A). Terminal antennomere with four large sensory cones located together inside a membranous area (Fig. 11C). Antennomere 5 latero-apically with four rows, antennomere 6 with three rows (Fig. 11B) of sensilla basiconica.

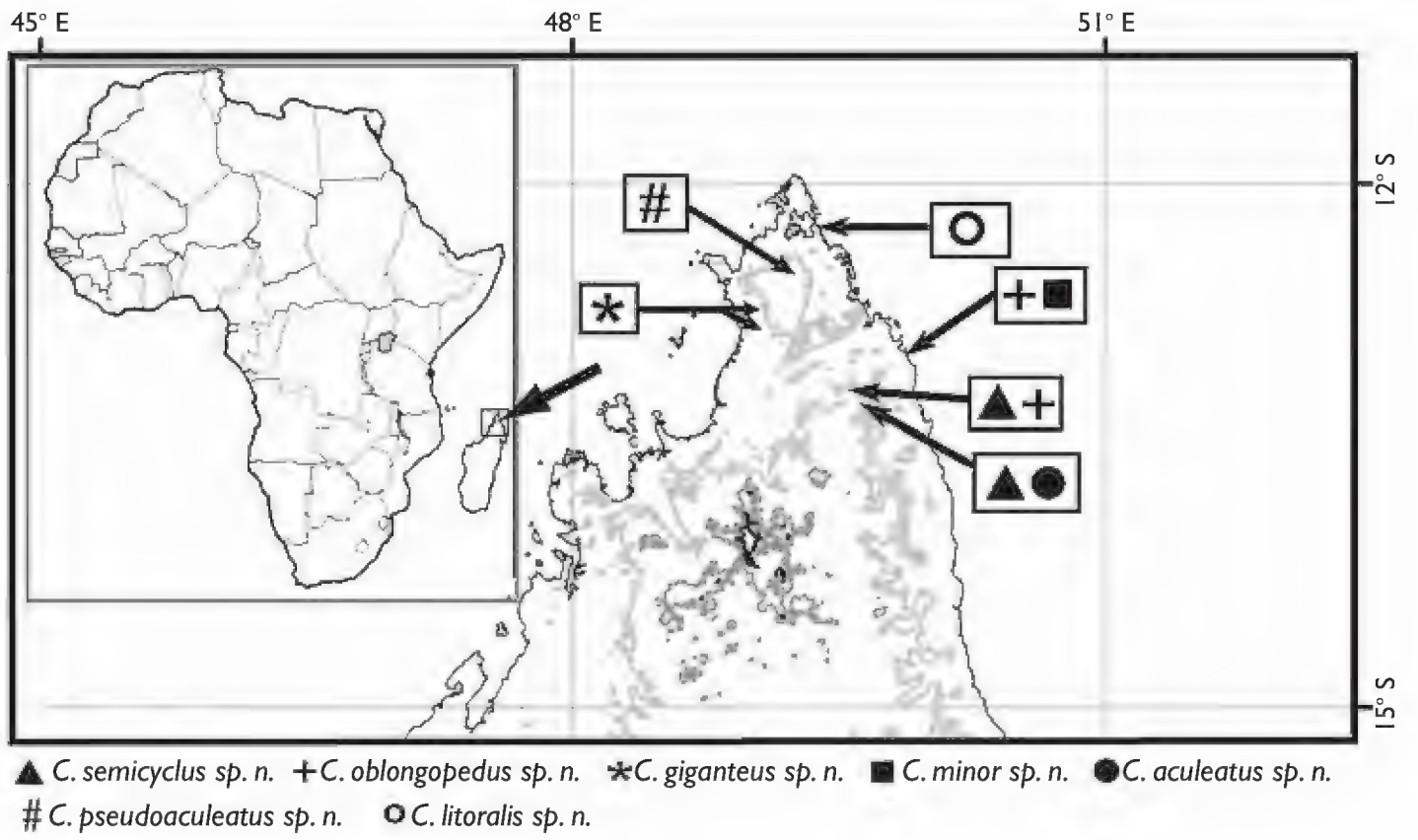


Figure 10. Distribution of the genus *Colossobolus* gen. n.

Figure 11. *Colossobolus semicyclus* sp. n., female paratype, SEM. **A** antenna, apical view **B** antennomere 5 with sensilla basiconica **C** apical view on disc **D** gnathochilarium, dorsal view. cp = central located pads, median palps; Endo = endochilarium; eP = external palpus; iP = internal palpus; sb =sensilla basiconica.

Gnathochilarium: of usual spirobolidan shape. Lamellae linguales each with two standard setae located behind one another. Stipites each with three apical setae (Fig. 13B). Mentum with several transverse ridges in basal half. Palpi of gnathochilarium with numerous sensilla. Hypopharyngeal crest with a field of spine-like structures.

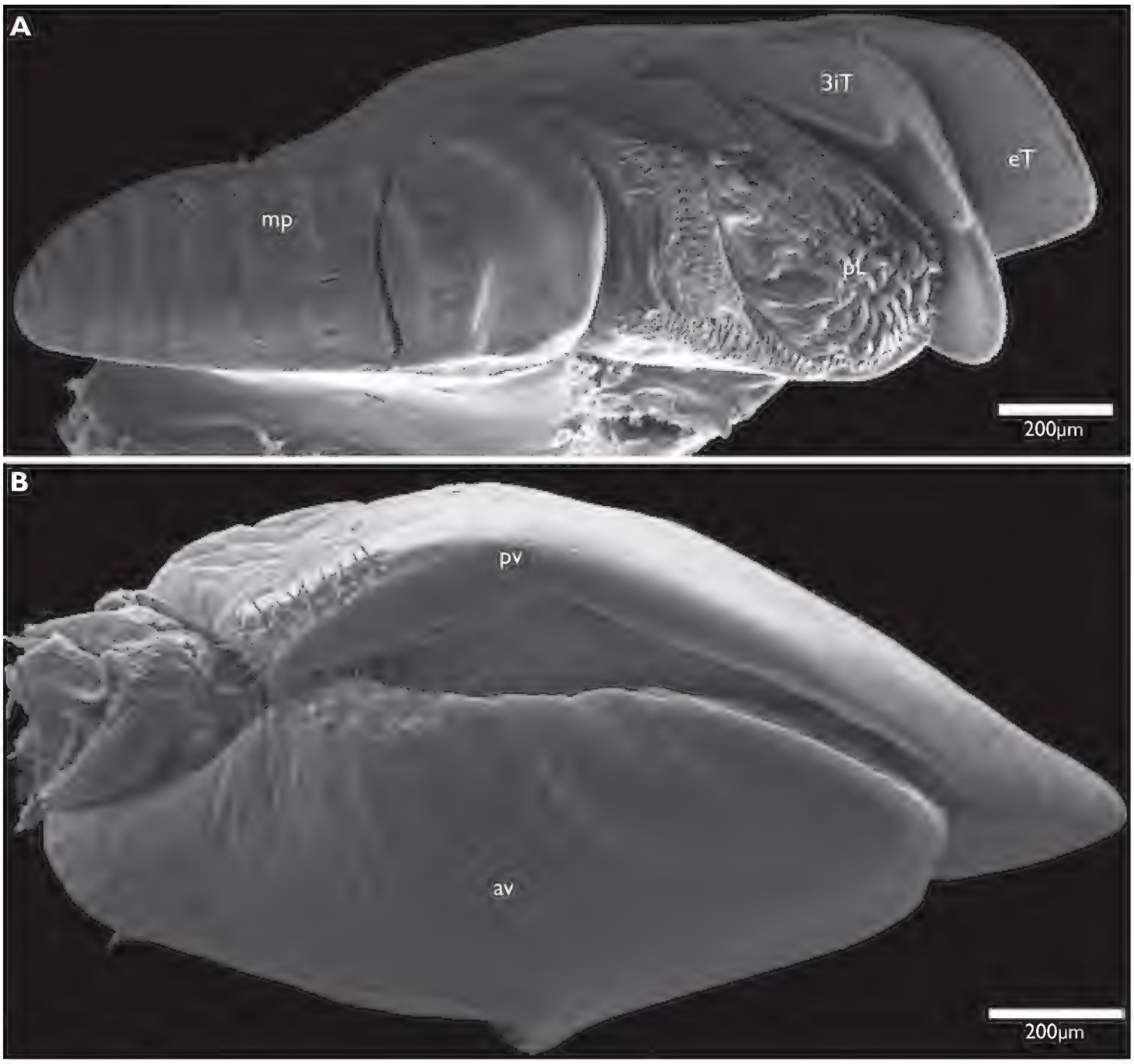


Figure 12. *Colossobolus semicyclus* sp. n., female paratype, SEM. **A** left mandible, mesal view **B** right vulva. 3iT = 3-combed internal teeth; av = anterior valve; eT = external tooth; mp = molar plate; pL = pectinate lamella; pv = posterior valve.

Central pads of endochilarium separated by a step into two levels, group of 10–12 sensilla located apically in recessed area. Medial palps with a large group of sensilla each, located towards hypopharyngeal crest (Fig. 11D).

Mandible: external tooth simple, rounded; mesal tooth with three cusps. Five pectinate lamellae. Mesal margin of pectinate area with circa four rows of small slender spines. Molar plate with numerous (7–10), very shallow transverse furrows (Fig. 12A).

Collum: smooth, laterally not protruding as far as ventral surface of body ring 2 (Figs 9A, B).

Body rings: mostly smooth, with some irregular punctation and some transverse impressions on mesozona. Metazona and mesozona ventrally with deep longitudinal impressions. Ozopores starting at ring 6, located closely in front of, but not touching suture between mesozona and metazona. Ozopore on ring 6 located much more ventrally than subsequent ozopores.

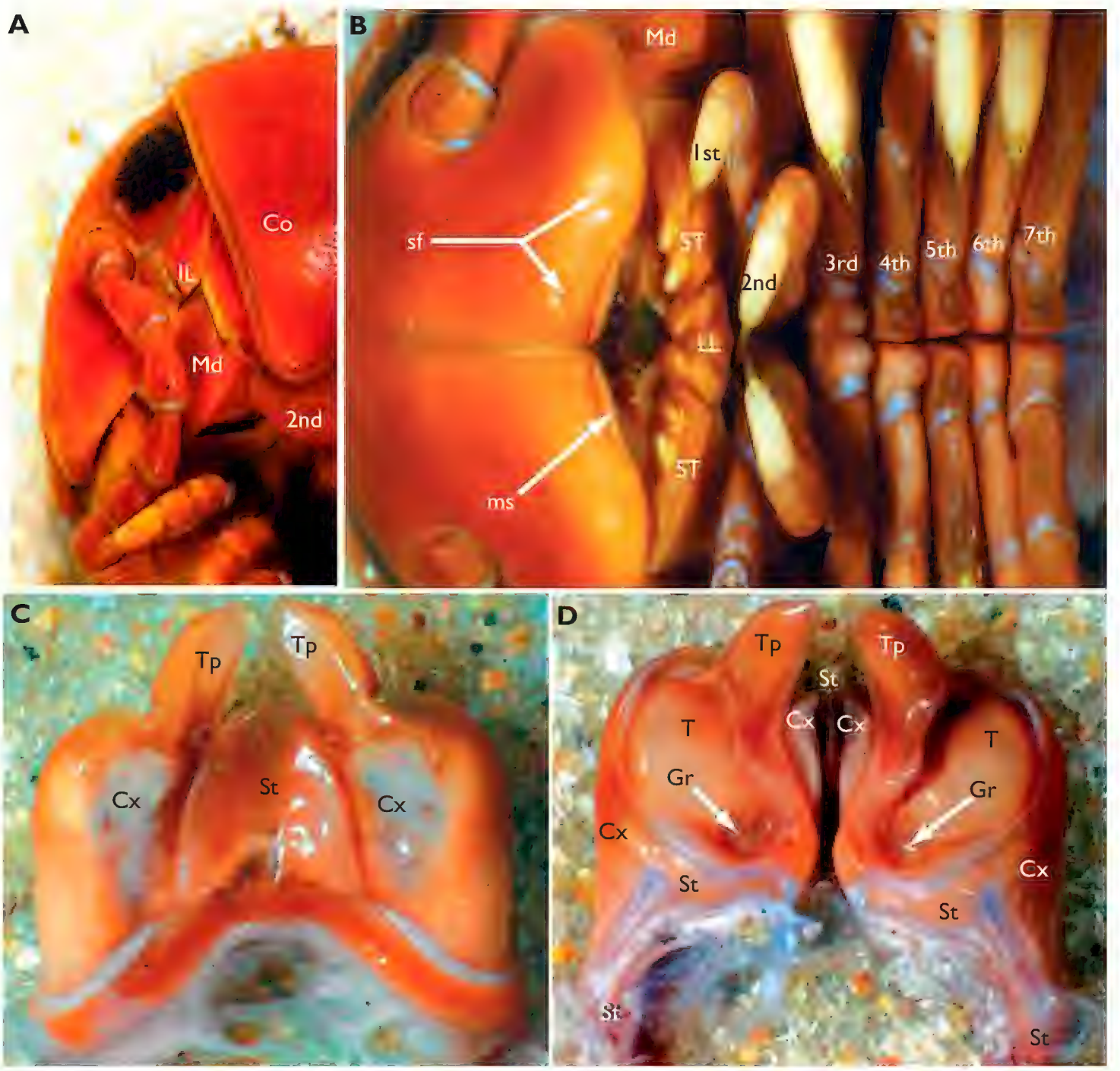


Figure 13. *Colossobolus oblongopedus* sp. n., male holotype. **A** head, lateral **B** legs 1–7, ventral view **C** anterior gonopods, anterior view **D** anterior gonopods, posterior view. Co = collum; Cx = coxite; Gr = groove on anterior gonopod; IL = incisura lateralis; LL = lamella lingualis; Md = mandible; ms = marginal setae; sf = setiferous foveolae; St = sternite; ST = stipites; T = telopodite; Tp = telopodite process. Not to same scale.

Telson: anal valves with well-developed lips and micropunctation, but with neither grooves nor setae. Preanal process well-rounded or sharp, but never extending beyond anal valves (Fig. 9C). Subanal scale inconspicuous.

Legs: coxae 1 and 2 elongated and fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae. Length of midbody legs circa 1.2 times body diameter in males, circa 0.8 times body diameter in females. Each podomere with an apical, ventral seta. Coxae 3 and beyond of rectangular shape (Fig. 18D). Tarsus with a stout dorso-apical setae and in males a pair of stout ventro-apical setae, in females with three pairs of setae, of which apical pair stout, others successively much smaller.

Male sexual characters: tarsi 3 and beyond with a large tarsal pad not protruding past base of claw. Coxae 3–7 with a short process each, this process protruding posteriorly, but never overlapping adjacent one. Processes on coxae 3 and 4 slightly longer than those on coxae 5–7 (Fig. 9B). Gonopods not projecting past body rings (Fig. 16A)

Anterior gonopods: sternite triangular, well-rounded or only slightly tapering (Fig. 9D), protruding almost as high as coxite. Coxite broad, smoothly rounded, laterally curving around telopodite, extending only slightly towards posterior side, where it is laterally visible as a small triangular sclerite (Fig. 9E). Mesal coxite process short, wide and well-rounded (Fig. 9D). Telopodite mesally elongated into a long, wide, well-rounded process (Fig. 9D). Mesal margin basally of telopodite process always elevated, sharp-edged, in some species widely protruding (Figs 9E, 18F). A large, deep groove usually present in basal part of telopodite (Fig. 13D). Apodeme very small, located basally of sternite and entirely covered with muscle tissue (Fig. 15C).

Posterior gonopods in situ almost completely covered by anterior gonopod. Posterior gonopods clearly divided into coxite and telopodite. Sternite sclerotized and well-visible (Fig. 15F). Coxite basally wide, mesally with a single groove (Fig. 14B) protruding into a stem towards telopodite. Telopodite always developed as a special disc, separated from coxite stem by a membranous area (Figs 9F–I). Telopodites either standing face-to-face (Figs 9F, G), or parallel (Figs 19A, B) to one another. Telopodite comprising of three components: (1) median membranous area, (2) lateral branch, (3) mesal main branch with membranous folds. Sperm canal discharging into membranous folds proximally on main branch. Telopodite in some species basally with a finger-shaped process, termed here as a "coxite branch" (Figs 9F, G). It is unclear whether the coxite branch belongs to the telopodite or coxite.

Female sexual characters: vulva simple, with a small, poorly sclerotized operculum at base, bivalve-like (Fig. 12B). Anterior valve shorter than posterior one. Both valves smooth, lacking sensory cones. Each valve basally towards opening with two or three rows of setae (Fig. 12B).

Etymology: *Colossobolus*, masculine, is composed of *colossus*, which refers to the extraordinary large size of species in this genus, and *-bolus*.

Key to the *Colossobolus* species:

1 Telopodite of posterior gonopod basally with a finger-shaped coxite branch (Figs 9C, 14A, 15F) **2**

– Telopodite of posterior gonopod lacking coxite branch (Figs 16F, 19A, 20G, 21E) **4**

2 Lateral branch of posterior gonopod telopodite curved towards coxite branch, almost forming a circle with latter (Figs 9H, I). Coxite of anterior gonopod in anterior view with a short, wide, well-rounded process (Fig. 9D) ..... ***C. semicyclus* sp. n.**

– Lateral branch of posterior gonopod telopodite straight (Fig. 14A). Coxite of anterior gonopod in anterior view with a short pointed process (Fig. 13C) **3**

3 Tarsi whitish (Fig. 13B). Collum completely red (Fig. 13A). Coxite branch of posterior gonopod short, half as long as lateral branch. Lateral branch irregularly curved, becoming apically thicker (Figs 14A, B). Retrorse process absent from mesal margin of telopodite process of anterior gonopod (Fig. 13D)..... ..... ***C. oblongopedus* sp. n.**

– Legs completely red (Fig. 15B). Collum at margins red, median part dark (Fig. 15A). Coxite branch of posterior gonopod long, as long as lateral branch. Lateral branch regularly curved (Fig. 15F). Mesal margin of telopodite process of anterior gonopod protruding into a very short, but pointed retrorse process (Fig. 15D) ..... ***C. giganteus* sp. n.**

4 Telopodites of posterior gonopods oriented face-to-face to one another. Main branch of telopodite overlapping juxtaposed counterpart (Figs 16E, F). Small, 85–100 mm long. Colour of body rings dark brownish (Fig. 16B).... ..... ***C. minor* sp. n.**

– Telopodites of posterior gonopods oriented parallel to one another. Telopodite main branches not overlapping (Figs 19A, B). Body large, >120 mm. Colour of body rings always partly red **5**

5 Mesal margin of telopodite process of anterior gonopod widely projecting, almost protruding up to lateral margin (Fig. 18F). Coxite process extraordinary long, but wide and well-rounded, longer than sternite, but far shorter than process of telopodite (Fig. 18E). Telopodite of posterior gonopod not U-shaped. Lateral branch weakly developed, very slender (Fig. 19A). Telopodite main branch separated into two parts, lateral part with large and long membranes, mesal part short and sclerotized. Telopodite lateral branch and both parts of main branch orientated parallel to one another (Figs 19A, B) ..... ***C. litoralis* sp. n.**

– Mesal margin of telopodite process of anterior gonopod sharp, but not projecting (Fig. 20F). Coxite process present, but short and well-rounded (Fig. 20A). Telopodite of posterior gonopod U-shaped (Fig. 20E). Lateral and main branches apically of similar width. Telopodite main branch not divided into two parts, branch basally sclerotized, apically membranous (Figs 20E, G) **6**

6 Preanal process apically sharp-edged, slightly shorter than anal valves (Fig. 20C). Main branch of posterior gonopod telopodite of equal width all along (Fig. 20E), longer than lateral branch (Fig. 20G) ..... ***C. aculeatus* sp. n.**

– Preanal process apically rounded, shorter than anal valves (Fig. 21B). Main branch of posterior gonopod telopodite basally very slender, but with a wide, swollen tip (Fig. 21E), shorter than lateral branch (Fig. 21F) .... ***C. pseudoaculeatus* sp. n.**

***Colossobolus semicyclus* Wesener, sp. n.**
urn:lsid:zoobank.org:act:8205B095-B802-46B7-8BA7-BEF078E551A8

Material examined: 2 ♂, 2 ♀, 1 imm. *Holotype:* 1 ♂ (120 mm long), CAS BLF 10114a. Madagascar, Province Antsiranana, Forêt d'Antsahabe, 11.4 km 275°W Daraina, tropical dry forest, 550 m, 13°12'42" S, 049°33'24" E, leg. B. L. Fisher et al., 12.XII.2003. *Paratypes:* 1 ♀, 1 imm., CAS BLF 10114a, same data as holotype; 1 ♂, 1 ♀, FMMC 5488, Province Antsiranana, near Analamozava River, 7.5 km SW Daraina, undisturbed humid lowland forest, 325–600 m, 13°15.3' S, 49°37.0' E, leg. S. Goodman, 3–10.XI.2001, pitfall trap.

Other material examined: 2 ♂, 1 ♀, CAS BLF 10877a, Forêt de Binara, 9.1 km SW Daraina, rainforest, 650–800 m, 13°15'48" S, 049°36'12" E, leg. B. L. Fisher, 19.XI.2004.

Differential diagnosis: *Colossobolus semicyclus* sp. n. cannot be separated from other sympatric *Colossobolus* species by external features alone (Fig. 10). Differs from all other species in the unique shape of the posterior gonopod telopodite (Figs 9F–I) and in the presence of a well-rounded coxite process on the anterior gonopod. Shares with *C. oblongopedus* sp. n. and *C. giganteus* sp. n. a finger-shaped coxite process on the posterior gonopods.

Description. *Measurements*: males with 49–52 body rings, circa 120 mm long, 9.7–11.4 mm wide. Females with 49–52 body rings, 100–125 mm long, 10.5–11.0 mm wide.

Coloration affected by alcohol. Head, legs, antennae and telson red. Meso- and metazonites of body rings reddish-brown, posterior margin with a thin, dark brown line (Figs 9A–C). *Antennae* protruding back to ring 3 (Fig. 9A). *Male coxal processes* present on coxae 3 and 4, well-developed. Coxae 5–7 with visible, but short processes (Fig. 9B).

Preanal process well-rounded, not projecting (Fig. 9C).

Anterior gonopod sternite elongated into a wide, broadly rounded lobe (Fig. 9D). Mesal process of coxite weakly developed, protruding into a short wide lobe which slightly extends beyond sternite (Fig. 9D). Telopodite on posterior side basally with a circular groove (Fig. 9E). Telopodite process long and relatively slender. Mesal margin laterally sharp-edged, but not projecting (Fig. 9E).

Posterior gonopods unique (Figs 9F–I). Telopodites positioned face-to face with one another. Coxite branch relatively short, wide and stout (Figs 9F–I). Lateral branch of telopodite curved, forming a 'C' together with coxite branch. Central membranous area protruding (Figs 9F, H). Mesal main branch well-developed, apical part overlapping lateral branch (Figs 9G, I). Mesal margin of main branch with two overlapping membranous folds. Membranous folds large, well-rounded, forming a half-circle (Figs 9G, I).

Intraspecific variation: animals from the type series (Forêt Antsahabe) differ greatly in size from those collected only some kilometers away in an area close to the Analamozava River. Specimens from the type series have 52 body rings while those

from the Analamozava River have only 49. Specimens from Antsahabe are approximately 10 mm longer but 1 mm slimmer than those from the Analamozava River. Males from both localities show identical gonopods. Those differences can probably be accounted for by the fact that the habitat on the Antsahabe site is much drier than the Analamozava River site. However, more specimens from both sites are necessary to further refine this intraspecific variation.

Distribution and ecology: this species has hitherto been recorded only in dry and subhumid forests at mid-altitudes (325–800 m) around Daraina (Fig. 10). *C. semicyclus* sp. n. occurs at Antsahabe sympatrically with *C. oblongopedus* sp. n., at the Analamozava river site sympatrically with *C. aculeatus* sp. n.

Etymology: *semicyclus*, adjective, refers to the uniquely shaped posterior gonopod telopodite.

Colossobolus oblongopedus Wesener, sp. n.

urn:lsid:zoobank.org:act:50DBF062-18CB-4A0A-AD61-10066B0A8604

Material examined: 9 ♂, 3 ♀ *Holotype:* 1 ♂ (126 mm long), CAS BLF 9429B, Madagascar, Province Antsiranana, Forêt d'Analabe, 30.0 km 72°ENE Daraina, 30 m, littoral rainforest, 13°05'00" S, 049°54'30" E, leg. B. L. Fisher, 27.XI.2003. *Paratypes:* 1 ♂, 1 ♀, CAS BLF 9429B, same data as holotype; 1 ♂, 1 ♀, CAS BLF 10114, Province Antsiranana, Forêt d'Antsahabe, 11.4 km 275°W Daraina, 550 m, tropical dry forest, 13°12'42" S, 049°33'24" E, leg. B. L .Fisher, 12.XII.2003, general collecting.

Other material examined: 4 ♂, 1 imm., FMMC, Madagascar, Prov. Antsiranana, Réserve Spéciale de Manongarivo, camp 1, 785 m, 13°58'38" S, 48°25'22" E, leg. S. M. Goodman, 28.II–6.III.1999; 1 ♀, FMMC, same data as previous; 2 ♂, FMMC, same data as previous.

Differential diagnosis: the general shape of the posterior gonopods of *Colossobolus oblongopedus* is similar to those of *C. giganteus* sp. n. The coxite branch is far shorter in *C. oblongopedus* than in *C. giganteus* sp. n. (compare Fig. 14A with Fig. 15E), while the telopodite main branch is more regularly shaped in the latter than in *C. oblongopedus* (compare Fig. 14B with Fig. 15F). The telopodite process of the anterior gonopod features a short, pointed, retrorse process in *C. giganteus* sp. n., which is entirely absent in *C. oblongopedus* (compare Fig. 13D with Fig. 15D). The collum is completely red in *C. oblongopedus* (Fig. 13A), while it is centrally dark in *C. giganteus* sp. n. (Fig. 15A).

Description. *Measurements*: males with 50–52 body rings, 120–148 mm long, 10.5–11.4 mm wide. Females with 50–52 body rings, 122–125 mm long, 10.5–12.6 mm wide.

Coloration affected by alcohol. Head, collum, antennae and telson red (Fig. 13A). Legs also red, but tarsi whitish (Fig. 13B). Meso- and metazonites of body rings reddish, posterior margin with a thin, dark brown line. *Antennae* protruding back to ring

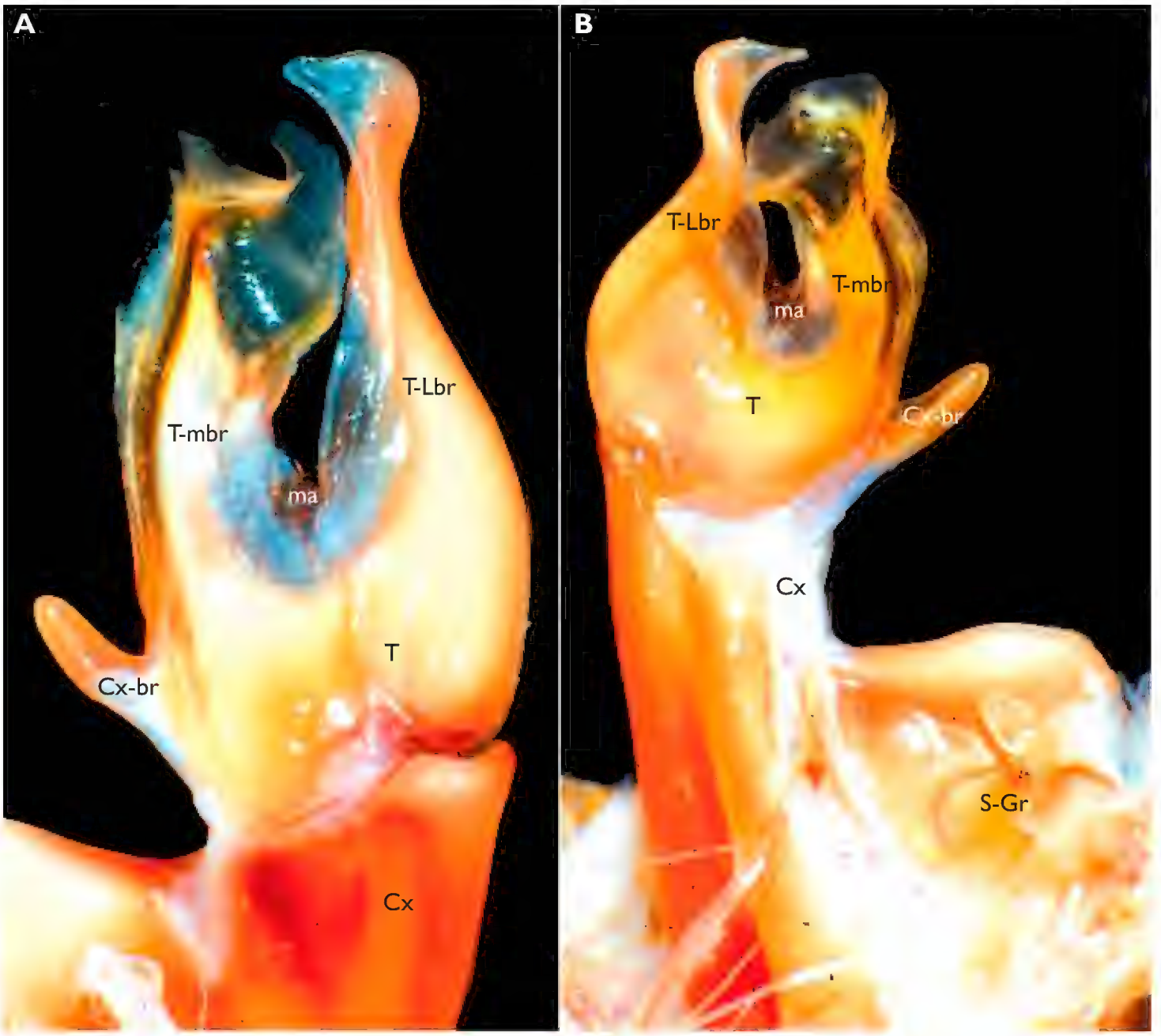


Figure 14. *Colossobolus oblongopedus* sp. n., male holotype, right posterior gonopod. **A** anterior view **B** posterior view. Cx = coxite; Cx-br = coxite branch; ma = membranous area; S-Gr = spermatic groove; T = telopodite; T-Lbr = telopodite lateral branch; T-mbr = telopodite main branch.

4. *Male coxal processes* on coxae 3 and 4 weakly developed, on coxae 5–7 barely visible (Fig. 13B). *Preanal process* well-rounded, not projecting.

Anterior gonopod sternite elongated into a wide, broadly rounded lobe (Fig. 13C). Mesal process of coxite weakly developed, protruding into a short, wide lobe with a pointed tip (Fig. 13C). Telopodite on posterior side basally with a circular groove (Fig. 13D). Telopodite process long and well-rounded (Fig. 13D), mesal margin laterally sharp, slightly protruding in basal half (Fig. 13D).

Posterior gonopods telopodites positioned parallel to one another. Coxite branch relatively short, wide, stout, less than half as long as lateral branch of telopodite (Figs 14A, B). Latter slightly curved, basally wide, at midpoint tapering, tip again wide and swollen (Fig. 14A). Central membranous area developed as a short, wide, well-rounded lobe (Fig. 14A). Mesal main branch short, basal part running parallel to lateral branch. Apical part of main branch extending towards and touching lateral branch (Fig. 14B). Mesal margin of main branch with two tiny, well-rounded, overlapping membranous

folds (Fig. 14A). Main branch laterally with a very large, irregular-shaped membrane (Figs 14A, B).

Intraspecific variation: the specimens from the dry forest Antsahabe (52 body rings) and Manangarivo (53 body rings) are slightly larger and more voluminous than the type series specimens from the littoral forest of Analabe, which possess 50 or 51 body rings. The gonopods from both populations are almost identical.

Distribution and ecology: *C. oblongopedus* occurs in the dry forest of Manangarivo, around Daraina and the tiny littoral forest fragment of Analabe (Fig. 10). Both areas are now isolated from one another by vast areas of pseudosteppe (Moat and Smith 2007). *C. oblongopedus* occurs in Analabe sympatric with *C. minor* sp. n., in Antsahabe together with *C. semicyclus* sp. n.

Etymology: *oblongopedus*, adjective, refers to the extraordinary long legs.

Colossobolus giganteus Wesener, sp. n.

urn:lsid:zoobank.org:act:AD9F0066-DFF2-4CDC-B39E-70CF2EC97F08

Material examined: 5 ♂, 2 ♀, 1 imm. Holotype: 1 ♂ (165 mm long), FMMC 6167, Madagascar, Province d'Antsiranana, RS d'Ankarana, Grotte des Chauves Souris, 3 km NW Mahamasina, 80 m, dry forest, 12°58'05.7" S, 049°07'09.6" E, leg. S. M. Goodman, 12.V.2003. *Paratypes:* 3 ♂, 1 ♀, 1 imm., FMMC 3920, RS Ankarana, 80 m, tropical dry forest, 12°54'32" S, 49°6'35" E, leg. B. L. Fisher et C. Griswold, 10–16. II.2001; 1 ♂, 1 ♀, MNHN noNumber, Province Diego-Suarez (Antsiranana), Rivière des Bois Pourris, Réc. A. Treha, 13.VII.1960.

Differential diagnosis: the gonopods of *C. giganteus* are so unique that they can only be confused with *C. oblongopedus*. See *C. oblongopedus* for a comparison of the two species.

Description. *Measurements*: males with 52 or 53 body rings, up to 165 mm long, 10.0–12.0 mm wide. Females with 52 body rings, of unknown length (broken), 10.3–15.5 mm wide.

Coloration affected by alcohol. Head, antennae, legs and telson red. Collum centrally dark (Fig. 15A). Meso- and metazonites of body rings reddish-brown. *Antennae* protruding back to ring 4. *Male coxal processes* on coxae 3 and 4 weakly developed, on coxae 5–7 short, barely visible (Fig. 15B). *Preanal process* well-rounded, not projecting.

Anterior gonopod sternite elongated into a wide, broadly rounded lobe. Apical part of lobe slightly more slender than remaining part (Fig. 15C). Mesal process of coxite weakly developed, protruding into a short, wide lobe with a pointed tip (Fig. 15C). Telopodite process long and well-rounded, basally at mesal margin with a minute, but sharp, lateral retrorse projection (Fig. 15D). Mesal margin laterally sharp-edged, not protruding (Fig. 15D).

Posterior gonopod telopodites positioned parallel to one another. Coxite branch long, wide and stout, almost as long as lateral branch of telopodite (Figs 15E, F). Lat-

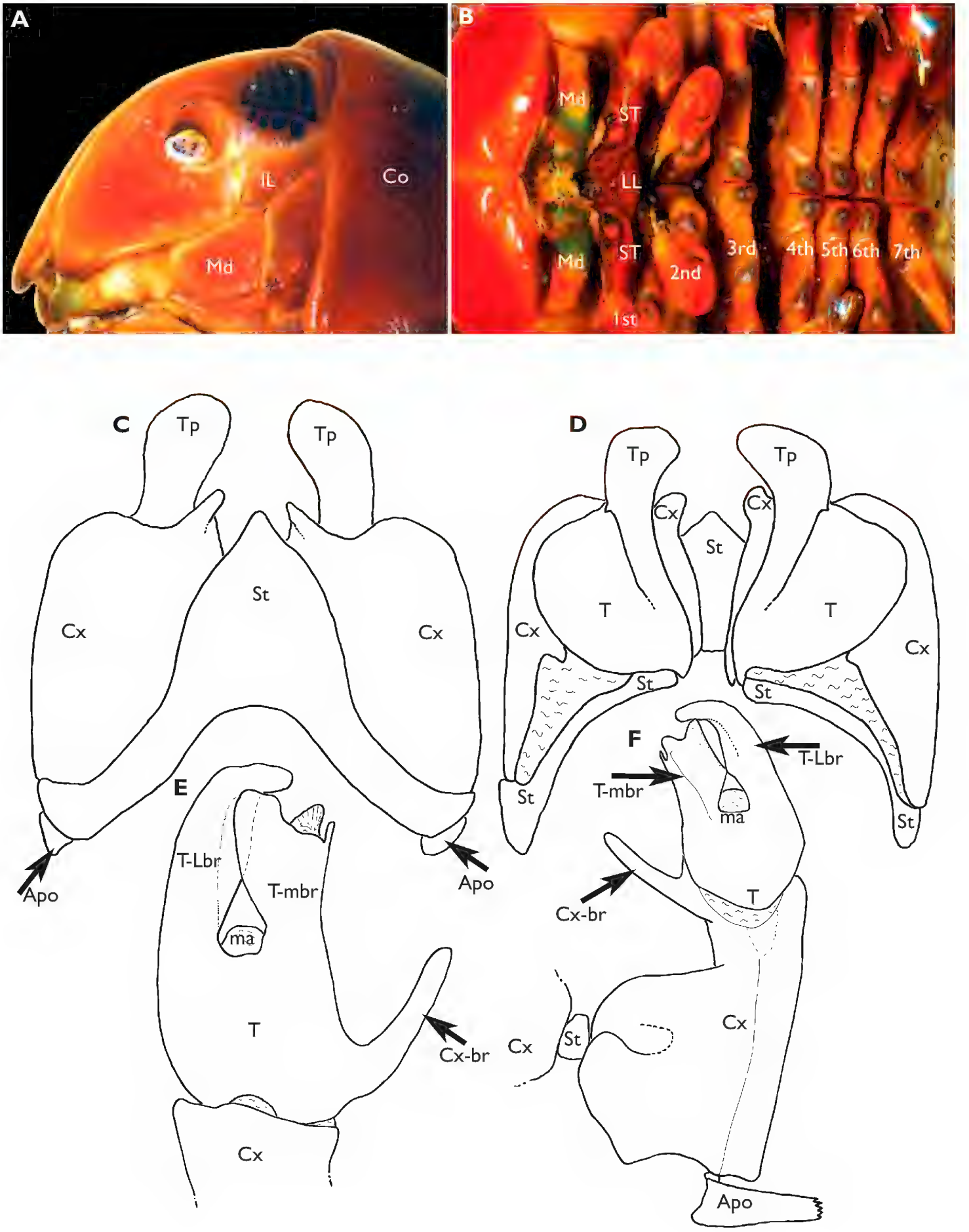


Figure 15. *Colossobolus giganteus* sp. n., male holotype. **A** head, lateral **B** legs 1–7, ventral view **C** anterior gonopods, anterior view **D** anterior gonopods, posterior view **E** left posterior gonopod, anterior view **F** left posterior gonopod, posterior view. Apo = apodeme; Co = collum; Cx = coxite; Cx-br = coxite branch; IL = incisura lateralis; LL = lamella lingualis; ma = membranous area; Md = mandible; St = sternite; ST = stipites; T = telopodite; T-Lbr = telopodite lateral branch; T-mbr = telopodite main branch; Tp = telopodite process. Not to same scale.

ter not tapering, apically slightly curved mesally (Fig. 15F). Central membranous area present as a short, wide, well-rounded lobe (Fig. 15E). Main branch shorter than lateral branch, both running parallel. Apical part of main branch extending towards and touching lateral branch (Fig. 15E). Inner margin of main branch with two very small, well-rounded, overlapping membranous folds. Main branch laterally with a very large irregularly shaped membrane (Fig. 15E).

Intraspecific variation: the specimens from the MNHN of unknown locality are 3–5 mm more slender than those from Ankarana.

Distribution and ecology: *C. giganteus* is only known from the dry forest of Ankarana (Fig. 10). The sample from the unknown locality from the MNHN suggests that *C. giganteus* has or had a wider distribution.

Etymology: *giganteus*, adjective, refers to the large size of the species. *Colossobolus giganteus* at 165 mm is the largest known species of the genus and one of the largest millipedes known from Madagascar.

***Colossobolus minor* Wesener, sp. n.**
urn:lsid:zoobank.org:act:BC5D77D7-9152-4DE3-94AA-CF2F1E83229C

Material examined: 5 ♂ *Holotype:* 1 ♂ (86 mm long), CAS BLF 9429-A, Madagascar, Province Antsiranana, Forêt d'Analabe, 30.0 km 72° ENE Daraina, 30 m, littoral rainforest, 13°05'00" S, 049°54'30" E, leg. B. L. Fisher, 27.XI.2003. *Paratypes:* 4 ♂, same data as holotype.

Differential diagnosis: the small size, dark body ring colour and uniquely-shaped, overlapping posterior gonopods of *C. minor* identify this species unambiguously.

Description. *Measurements*: males with 47 body rings, 84–100 mm long, 8.6–9.4 mm wide. Females unknown.

Coloration affected by alcohol. Head, antennae, legs and telson red (Figs 16A, B). Pro- and mesozona dark brown, posterior half of metazona red. *Antennae* protruding back to ring 3. *Male coxal processes* on coxae 3–5 weakly developed, on coxae 6 and 7 barely visible (Fig. 16A). *Preanal process* well-rounded (Fig. 16B).

Anterior gonopod sternite elongated into a wide, broadly rounded lobe (Fig. 16C). Mesal process of coxite weakly developed, protruding into a short, wide lobe with a well-rounded tip (Fig. 16C). Telopodite basally with a groove (Fig. 16D). Telopodite process long and well-rounded. Mesal margin laterally sharp-edged, at midpoint slightly protruding (Fig. 16D).

Posterior gonopod telopodites positioned face-to-face to one another. Coxite branch absent (Fig. 16E), lateral branch of telopodite straight, tapering (Fig. 16E). Central membranous area present as a short, wide, well-rounded lobe (Fig. 16E). Main branches of both posterior gonopods overlapping each other (Figs 16E, F). Main branch shorter than lateral branch, former at half of its length dividing into two parts, a mesal sclerotized finger-shaped process and a lateral wider membranous part (Figs 16E, F). Finger-shaped processes of both posterior gonopods overlap each others membranous parts (Fig. 16E).

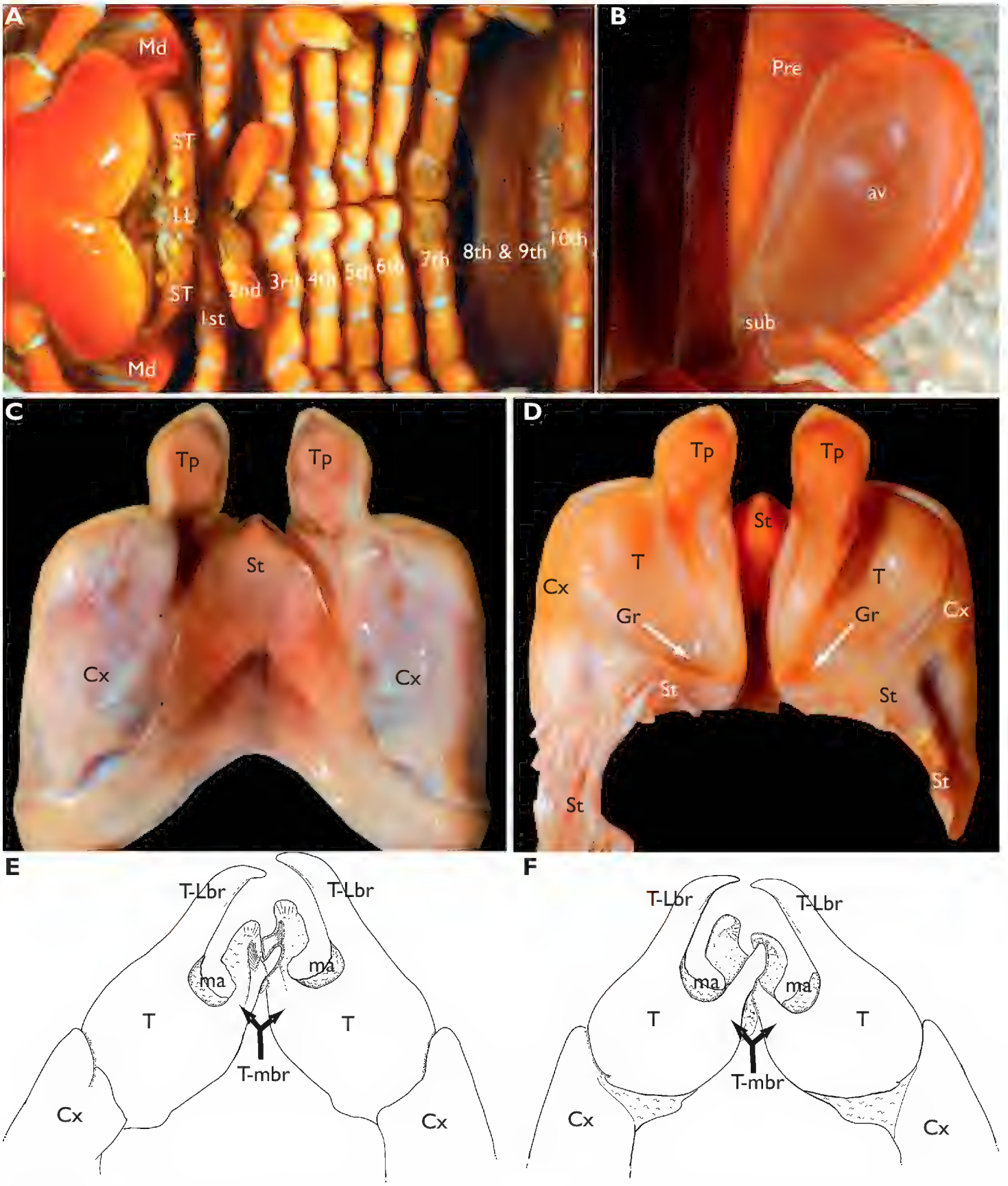


Figure 16. *Colossobolus minor* sp. n., male holotype. **A** legs 1–7, ventral view **B** telson **C** anterior gonopods, anterior view **D** anterior gonopods, posterior view **E** left posterior gonopod, anterior view **F** left posterior gonopod, posterior view. av = anal valves; Cx = coxite; Gr = groove on anterior gonopods; LL = lamella lingualis; ma = membranous area; Md = mandible; Pre = preanal ring; St = sternite; ST = stipites; sub = subanal scale; T = telopodite; T-Lbr = telopodite lateral branch; T-mbr = telopodite main branch; Tp = telopodite process. Not to same scale.

Distribution and ecology: *C. minor* is only known from the littoral forest of Analabe (Fig. 10), occurring sympatric with the larger *C. oblongopedus*.

Etymology: *minor*, adjective, refers to the small size of the species. *Colossobolus minor* is the smallest known species of the genus.

***Colossobolus litoralis* Wesener, sp. n.**
urn:lsid:zoobank.org:act:A031F0AE-D22A-42D8-BFDF-A34F137425AA

Material examined: 4 ♂, 1 ♀ *Holotype:* 1 ♂ (132 mm long), ZSM FGZC 1705, Madagascar, Province Antsiranana, Forêt d'Orangea, 10 m, littoral rainforest, 12°15' S, 49°22' E, leg. S. Megson, 20.II.2008, pitfall trap. *Paratypes:* 3 ♂, 1 ♀, FMMC 3919, Forêt d'Orangea, 90 m, littoral rainforest, 12°15'32" S, 49°22'29" E, leg. Fisher, Griswold et al., 22–28.II.2001.

Differential diagnosis: the special-shaped anterior and posterior gonopods of *C. litoralis* are a unique character.

Description. *Measurements*: males with 51 body rings, 132–138 mm long, 11.0–11.6 mm wide. Female with 51 body rings, 128 mm long, 12.9 mm wide.

Coloration affected by alcohol. Head, antennae, legs and telson red (Fig. 17). Pro- and anterior part of mesozona dark brown, posterior part of meso- and metazonites red.

Figure 17. *Colossobolus litoralis* sp. n., living specimen, photographed by Angelika Knoll, February 2007 at Forêt Orangea (all rights reserved).

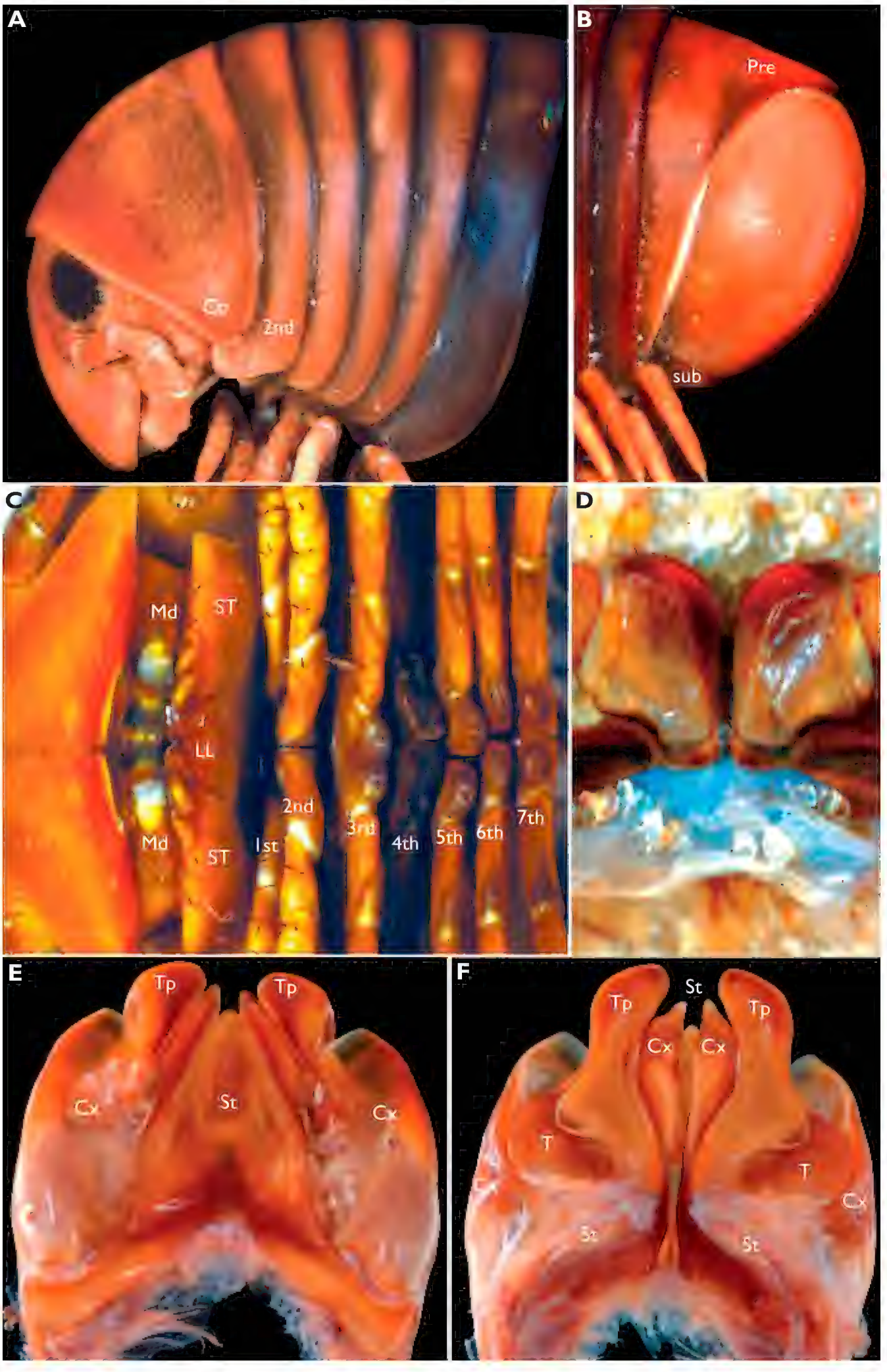


Figure 18. *Colossobolus litoralis* sp. n., male holotype. **A** head, lateral **B** telson **C** legs 1–7, ventral view **D** coxae of midbody leg, posterior view **E** anterior gonopods, anterior view **F** anterior gonopods, posterior view. av = anal valves; Co = collum; Cx = coxite; LL = lamella lingualis; Md = mandible; Pre = preanal ring; St = sternite; ST = stipites; sub = subanal scale; T = telopodite; Tp = telopodite process. Not to same scale.

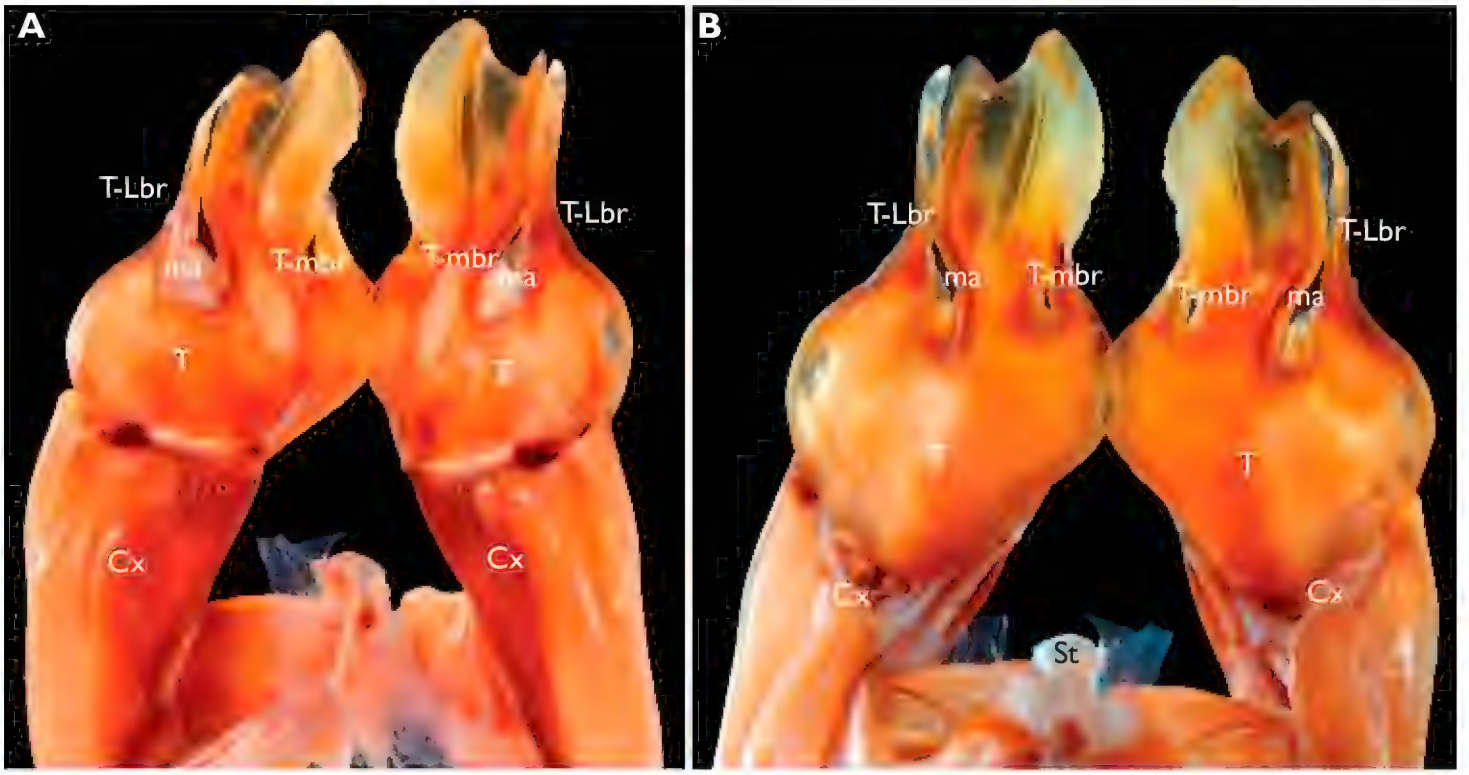


Figure 19. *Colossobolus litoralis* sp. n., male holotype, posterior gonopods. **A** anterior view **B** posterior view. Cx = coxite; ma = membranous area; S = sternite; T = telopodite; T-Lbr = telopodite lateral branch; T-mbr = telopodite main branch.

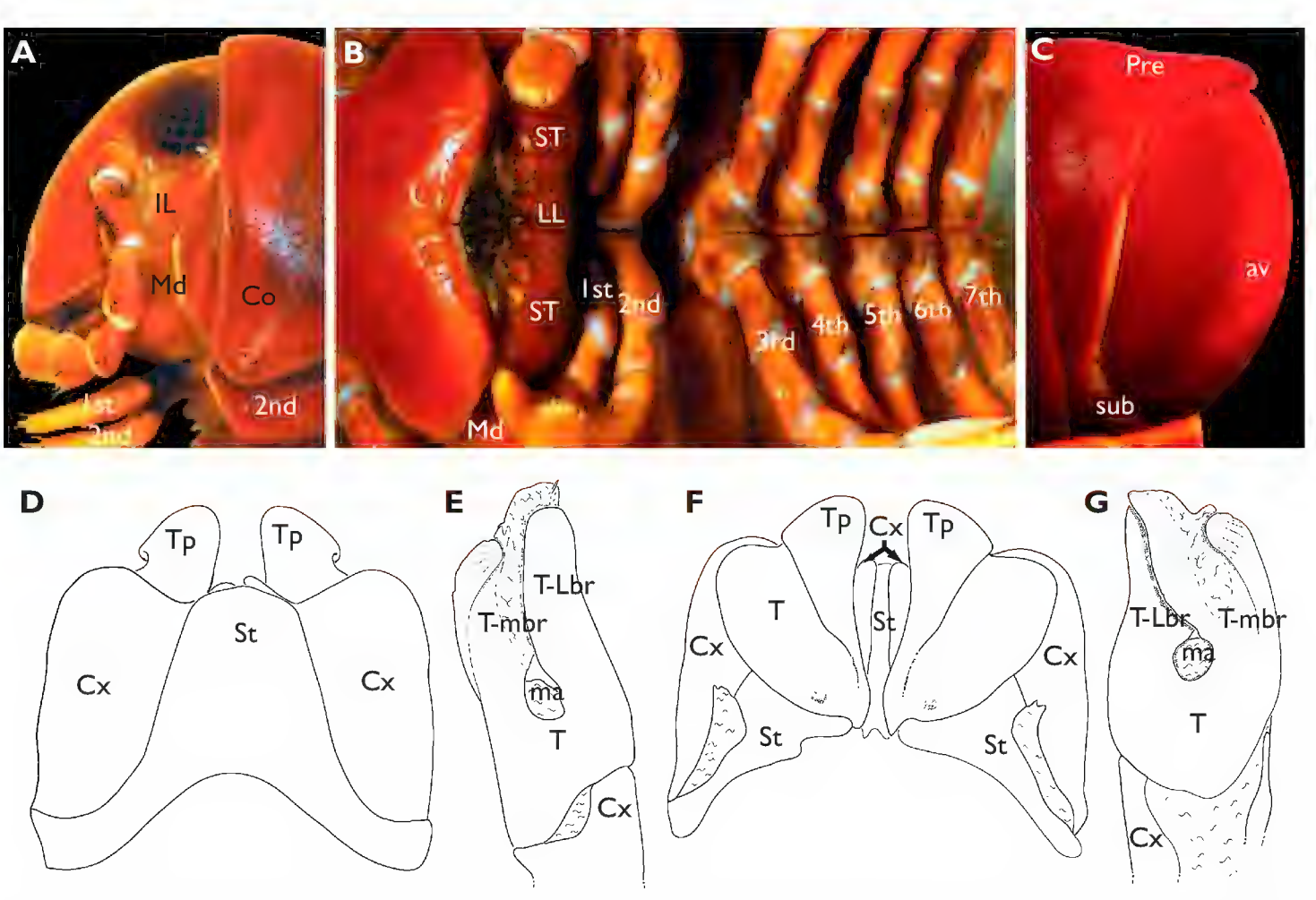


Figure 20. *Colossobolus aculeatus* sp. n., male holotype. **A** head, lateral **B** legs 1–7, ventral view **C** telson **D** anterior gonopods, anterior view **E** right posterior gonopod, anterior view **F** anterior gonopods, posterior view **G** right posterior gonopod, posterior view. av = anal valves; Co = collum; Cx = coxite; IL = incisura lateralis; LL = lamella lingualis; ma = membranous area; Md = mandible; Pre = preanal ring; St = sternite; ST = stipites; sub = subanal scale; T = telopodite; T-Lbr = telopodite lateral branch; T-mbr = telopodite main branch; Tp = telopodite process. Not to same scale.

Antennae protruding back to ring 3 (Fig. 18A). *Male coxal processes* on coxae 3 and 4 weakly developed, on coxae 5–7 barely visible (Fig. 18C). *Preanal process* well-rounded, not projecting (Fig. 18B).

Anterior gonopod sternite elongated into a wide, broadly rounded lobe (Fig. 18E). Mesal process of coxite prominent, protruding into a long wide lobe with a well-rounded tip, lobe only slightly shorter than telopodite process (Fig. 18E). Telopodite process long and well-rounded. Mesal margin laterally sharp, at mid-length conspicuously protruding into a long and well-rounded process (Fig. 18F).

Posterior gonopod telopodites positioned parallel to one another. Coxite branch absent (Fig. 19A). Telopodite lateral branch very slender, straight, tapering towards pointed tip (Fig. 18A). Central membranous area present as a short, wide, well-rounded knob (Fig. 19B). Main branch much longer than lateral branch, basally divided into two parts. Inner part developed as a short, slender, sclerotized process, apically tapering, with a pointed tip. Lateral part prominently elongated into large, flag-like membranous areas, extending beyond telopodite (Figs 19A, B).

Distribution and ecology: *C. litoralis* is only known from the littoral forest of Forêt d'Orangea (Fig. 10).

Etymology: *litoralis*, adjective, refers to the only known site were this species occurs, the littoral forest of Forêt d'Orangea.

***Colossobolus aculeatus* Wesener, sp. n.**
urn:lsid:zoobank.org:act:FA93B3D8-7AD7-4E8F-93E9-CA4B329D4BB9

Material examined: 2 ♂ *Holotype:* 1 ♂ (122 mm long), CAS BLF 9555, Madagascar, Province Antsiranana, Forêt de Binara, 7.5 km 230° SW Daraina, 375 m, tropical dry forest, 13°15'18"S, 049°37'00"E, leg. B. L. Fisher, 1.XII.2003. *Paratype:* 1 ♂, same data as holotype.

Similar species: the special U-shaped posterior gonopods are unique for *Colossobolus* except for *C. pseudoaculeatus* sp. n. *C. aculeatus* differs from the latter in the presence of a sharp-ending preanal process, which is well-rounded in *C. pseudoaculeatus* sp. n. (compare Fig. 20C with Fig. 21B). The lateral branch of the posterior gonopod telopodite is of equal width all along in *C. aculeatus* while it is basally slender with a swollen tip in *C. pseudoaculeatus* sp. n. (compare Fig. 20E with Fig. 21E).

Description. *Measurements*: males with 51 body rings, circa 122 mm long, 9.5 mm wide. Female unknown.

Coloration affected by alcohol. Head, antennae, legs and telson red (Figs 20A–C). Median part of collum dark, margins red (Fig. 20A). Pro- and anterior part of mesozonites dark brown, posterior part of meso- and metazonites red. *Antennae* protruding back to ring 3. *Male coxal processes* on coxae 3 and 4 barely visible, on coxae 5–7 absent (Fig. 20B). *Preanal process* sharp-edged, but not projecting over anal valves (Fig. 20C).

Anterior gonopod sternite elongated into a wide, broadly rounded lobe (Fig. 20D). Mesal process of coxite weakly developed, protruding into a very short wide lobe with

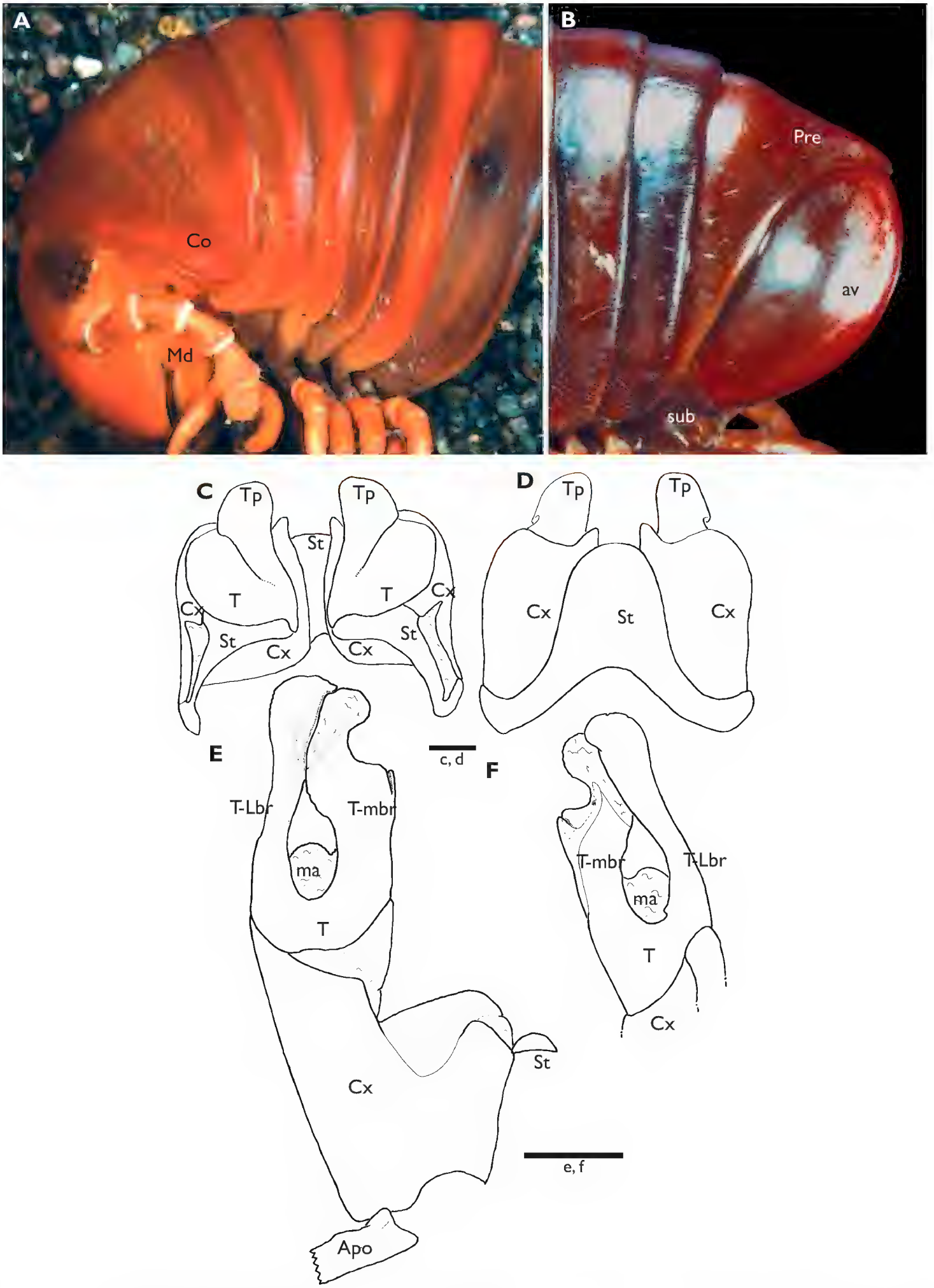


Figure 21. *Colossobolus pseudoaculeatus* sp. n., male holotype. **A** head, lateral **B** telson **C** anterior gonopods, posterior view **D** anterior gonopods, anterior view **E** right posterior gonopod, posterior view **F** right posterior gonopod, anterior view. Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; ma = membranous area; Md = mandible; Pre = preanal ring; St = sternite; sub = subanal scale; T = telopodite; T-Lbr = telopodite lateral branch; T-mbr = telopodite main branch; Tp = telopodite process. Not to same scale.

a well-rounded tip. Lobe only slightly longer than sternite (Fig. 20D). Telopodite process long, becoming apically thicker than basally. Mesal margin laterally sharp, not projecting (Fig. 20F).

Posterior gonopods telopodites positioned parallel to one another, generally U-shaped (Figs 20E, G). Coxite branch absent (Fig. 20E). Lateral branch of regular width, tip wide, well-rounded, not thicker than median or basal parts (Fig. 20E). Central membranous area present as a wide, well-rounded knob (Fig. 20G). Main branch slightly longer than lateral branch, latero-apically towards lateral branch with a large membranous area (Fig, 20G).

Distribution and ecology: *C. aculeatus* is only known from the Forêt Binara (Fig. 10) where it occurs in close proximity to *C. semicyclus*.

Etymology: *aculeatus*, adjective, refers to the sharp-edged preanal process, unique for *Colossobolus*.

***Colossobolus pseudoaculeatus* Wesener, sp. n.**
urn:lsid:zoobank.org:act:2C06B20E-C62D-4CAE-9030-0761193A9DE9

Material examined: 1 ♂ *Holotype:* 1 ♂ (119 mm long), ZSM FGZC 1847, Madagascar, Province Antsiranana, Forêt d'Ambre, Provate Reserve Le Fontenay, leg. Köhler and Franzen, 26.II.2008.

Differential diagnosis: the anterior and posterior gonopods of *C. pseudoaculeatus* sp. n. can only be confused with those of *C. aculeatus*. See the latter for a list of the characters distinguishing these two species.

Description. *Measurements*: male with 49 body rings, circa 119 mm long, 9.55 mm wide. Female unknown.

Coloration affected by alcohol. Head, antennae, legs and telson red (Figs 21A, B). Median part of collum dark, margins red (Fig. 21A). Body rings anteriorly dark brown, posteriorly wine-red. *Antennae* protruding back to ring 4. *Male coxal processes* present on coxae 3 and 4, on coxae 5–7 absent. *Preanal process* well-rounded, not projecting over anal valves (Fig. 21B).

Anterior gonopod sternite elongated into a wide, broadly rounded lobe (Fig. 21D). Mesal process of coxite weakly developed, protruding into a very short wide lobe with a well-rounded tip; lobe only slightly longer than sternite (Fig. 21D). Telopodite process long and well-rounded, apically thicker than basally. Mesal margin laterally sharp, not projecting (Fig. 21C).

Posterior gonopods telopodites positioned parallel to one another, generally U-shaped (Figs 21E, F). Coxite branch absent (Fig. 21E), lateral branch basally slender, width apically increasing (Figs 21E, F); tip swollen, slightly curved mesally (Fig. 21E). Central membranous area present as a wide, well-rounded knob (Fig. 21E). Main branch slightly shorter than lateral branch, latero-apically towards lateral branch with a large membranous area (Figs 21E, F).

Distribution and ecology: *C. pseudoaculeatus* is only known from the Forêt d'Ambre (Fig. 10).

Etymology: *pseudoaculeatus*, adjective, refers to the close similarity of the species to *Colossobolus aculeatus*.

Zehntnerobolus Wesener, gen. n.

urn:lsid:zoobank.org:act:644F0D35-7FF2-4F9B-B5C9-6ADC49F512B8

Type species: *Spirobolus rubripes* de Saussure & Zehntner, 1897, monotypic

Diagnosis: telopodite process of anterior gonopod slender and laterally curved, a unique character of *Zehntnerobolus* gen. n. Telopodite of posterior gonopod of unique shape, sperm canal protruding above lateral margin at mid-length (Figs 22E, F). Suspicious row of sclerotized nodules located just below point where sperm canal protrudes above lateral margin (Fig. 22G). Shares a small body size (30–36 mm) and large male coxal processes on coxae 3–5 only with *Spiromimus* de Saussure & Zehntner, 1901 (Wesener and Enghoff, 2009). Telopodite of anterior gonopod at lateral margin elevated (Fig. 22E), similar to *Pseudocentrobolus* gen. n. and *Granitobolus* gen. n. Discharge opening of sperm canal turned laterally (Figs 22E, F), like in *Alluviobolus* gen. n. and *Riotintobolus* gen. n.

Distribution and ecology: only known from the East Malagasy rainforests of Andrangoloaka and 30 km SE in Moramanga. Since 1900 no additional specimens have been collected. The reddish-black colour pattern plus medium length antennae and legs might indicate a life on the surface of (or inside) the leaf-litter.

Etymology: *Zehntnerobolus*, masculine, is composed of *Zehntner*, after Dr. Leo Zehntner (1864–1961), who described numerous millipede species from Madagascar, including the type species of this genus, and *-bolus*.

Zehntnerobolus rubripes (de Saussure & Zehntner, 1897), comb. n.

Spirobolus rubripes de Saussure & Zehntner, 1897: plate XI, fig. 48, plate XII, fig. 6.
Spirostrophus rubripes, de Saussure and Zehntner 1902: 154.
NOT *Spirostrophus rubripes* Attems, 1927: 64
Spirostrophus rubripes, Enghoff 2003: 624 (lists species name).

Comments: drawings of *Zehntnerobolus rubripes* were first published under the name *Spirobolus rubripes* (de Saussure & Zehntner, 1897). *Spirobolus* is an East Asian genus. So, when publishing the text description in 1902, de Saussure and Zehntner put *S. rubripes* in the newly erected genus *Spirostrophus*, which included a non-related assemblage of species. However, they already noted: "Le *S. rubripes* offre de caractères un peu aberrantes: il est par conséquent difficile à classer. [...]. La position de cette espèce est donc incertaine." (de Saussure and Zehntner 1902: 158). They, unfortunately, did not put *S. rubripes* into a new genus. The description of *Spirostrophus rubripes* by de

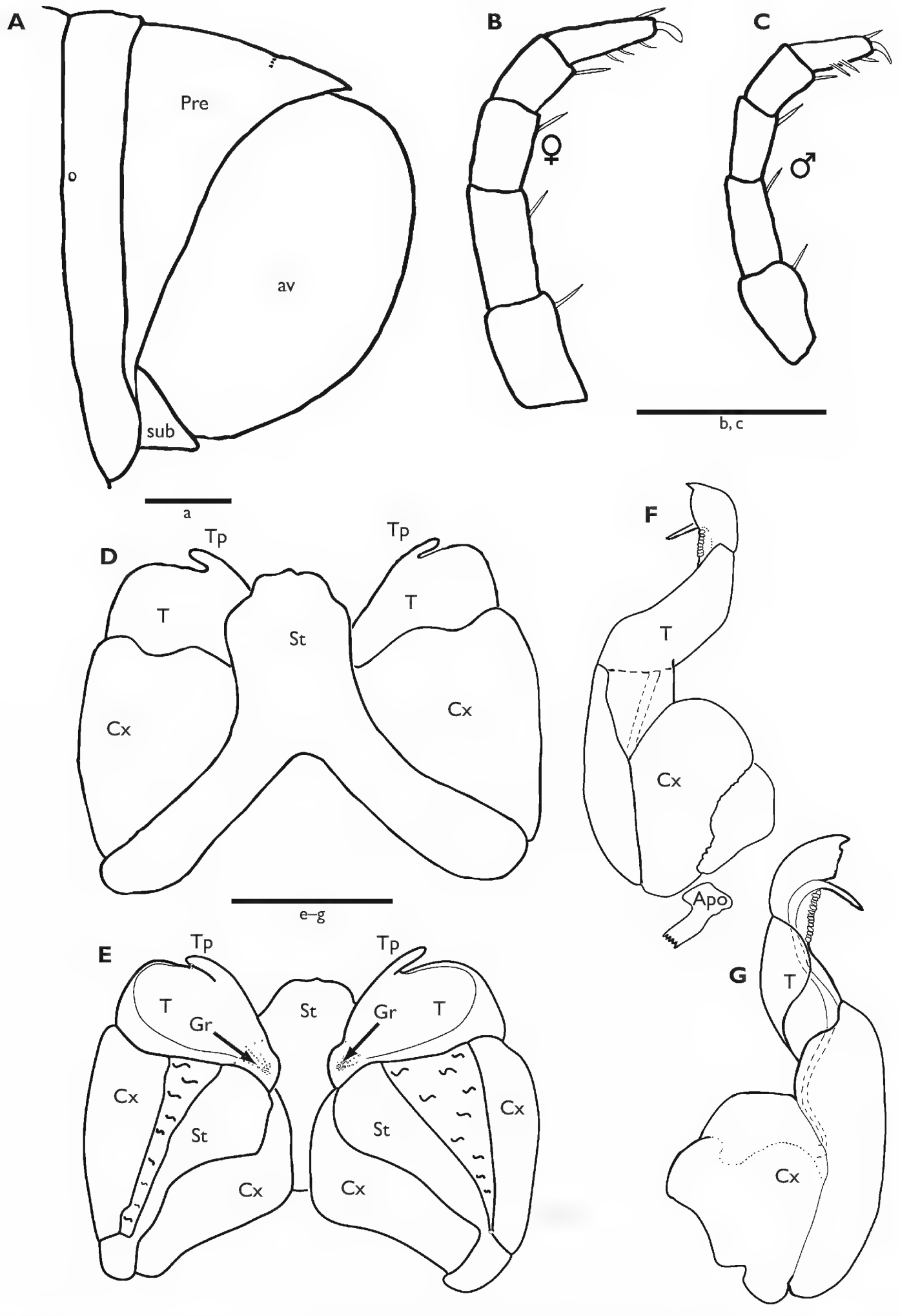


Figure 22. *Zehntnerobolus rubripes* comb. n., A, C–G male lectotype, B female paratype, **A** telson **B, C** right midbody leg **D** anterior gonopod, anterior view **E** anterior gonopod, posterior view **F** left posterior gonopod, anterior view **G** left posterior gonopod, posterior view. Apo = apodeme; av = anal valves; Cx = coxite; Gr = groove; Pre = preanal ring; St = sternite; sub = subanal scale; T = telopodite; Tp = telopodite process. Scale bars = 1 mm.

Saussure and Zehntner was obviously all but forgotten, because Attems also named a non-related species from Indonesia *Spirostrophus rubripes* Attems, 1927. The type species of the genus *Spirostrophus* is now regarded as a synonym of the type species of the East Indian genus *Leptogoniulus* Silvestri, 1897 (Hoffman 1980, Shelley and Lehtinen 1999). *Spirostrophus rubripes* (de Saussure & Zehntner, 1897 shares no characters with *Leptogoniulus*, therefore a new genus had to be established to incorporate this species.

Material examined: 2 ♂, 2 ♀ *Lectotype:* designated herewith to fix the concept of *Zehntnerobolus rubripes* (de Saussure & Zehntner, 1897) and to ensure the universal and consistent interpretation of the same: ♂ (dissected, 30 mm long), MNHN HB049. Madagascar, Province Toamasina, Forêt de Moramanga, rainforest, 18°56'20" S, 48°13'40" E, leg. Musée de Genève, det. de Saussure, 1903. *Paratypes:* 1 ♂, 2 ♀, MNHN HB049, same data as lectotype.

Additional locality data from the literature: de Saussure and Zehntner 1902: Madagascar, Forêt d'Andrangoloaka, rainforest, 19°2'0.00" S, 47°55'0.12" E, leg. Franz Sikora (1886–1892).

Description. *Measurements*: males with 38 or 39 rings, circa 32 mm long, 2.9 mm wide. Females with 39 or 40 rings, 36–37 mm long, 3.7 mm wide.

Coloration decolorized in alcohol. Head, antennae and legs red (according to drawing and original description). Body ventrally and dorsally on meso- and metazonites pitchblack. Mesozonites dorsolaterally blood-red (see de Saussure and Zehntner 1897: plate XI, fig. 48).

Head: each eye with circa 26–28 ocelli arranged in 6 or 7 vertical rows. Labrum with standard three irregular teeth and a single row of 10–12 stout marginal setae. Clypeus with two setiferous foveolae on each side. Antennal cavity absent. Antennae of medium length, protruding back to ring 4 in females, ring 5 in males. Relative lengths of antennomeres: 1<<2=3=4=5=6. Terminal antennomere with four large sensory cones located together inside a membranous area. Antennomere 5 latero-apically with five rows, antennomere 6 with four rows of sensilla basiconica.

Gnathochilarium: of usual spirobolidan shape. Lamellae linguales each with two standard setae located behind one another. Stipites each with three apical setae. Basal parts could not be studied because a dissection was not attempted. *Mandible* not dissected.

Collum: smooth, laterally not protruding as far as ring 2.

Body rings: mostly smooth, with some transverse impressions on mesozona. Ozopores starting at ring 6, located closely in front of, but not touching suture between mesozona and metazona.

Telson: anal valves with neither lips, nor micropunctation. Preanal process sharp, but not protruding above anal valves (Fig. 22A).

Legs: coxae 1 and 2 elongated and fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae. Length of midbody legs circa 0.8 times body diameter in females (Fig. 22B), circa 1.0 times body diameter in males (Fig. 22C). Each podomere ventrally with an apical seta. Coxae 3 and beyond of cylindrical shape. Tarsus with a stout dorso-apical seta and three pairs of regular ventral spines.

Male sexual characters: tarsal pads absent (Fig. 22C). Coxae 3–5 each with a large conical coxal process, protruding posteriorly to coxa 6.

Anterior gonopod sternite elongated into a wide, rounded lobe, apically with three very short, well-rounded tips (Fig. 22D). Mesal process of coxite absent. Telopodite on posterior side basally with a circular groove (Fig. 22E). Telopodite process slender and short, curved laterally (Fig. 23E). Lateral margin elevated (Fig. 22E).

Posterior gonopods unique (Figs 22F, G). Gonopod pair connected by a sclerotized and visible sternite. Telopodites positioned parallel to one another, sperm canal discharging laterally (Fig. 23G). Coxite and telopodite separated by a suture; coxite with a single groove. Telopodite with torsion, tip of telopodite curved laterally, with a sharp-edged tip (Fig. 22F). Sperm canal laterally strongly projecting over telopodite margin (Fig. 22G). Basally of projection of sperm canal with a row of sclerotized nodules (Fig. 22G). Sperm canal running through coxite at mesal, through telopodite at lateral margin (Fig. 22G).

Female sexual characters: vulva simple, bivalve-like.

Intraspecific variation: the measurements of the type series fit in very well with those recorded in the literature (de Saussure and Zehntner 1902: 159).

Remark

The mentum is subdivided by a strong transverse ridge separating a basal, transversely striate part and an apical, smooth part, which is recessed when the gnathochilarium is viewed from below in all the following genera. Such a subdivision is unique within the whole order Spirobolida.

Genera with subdivided mentum
Flagellobolus, gen. n.
Riotintobolus gen. n.
Pseudocentrobolus gen. n.
Granitobolus gen. n.
Caprobolus gen. n.
Alluviobolus gen. n.
Ostinobolus gen. n.

Flagellobolus Wesener, gen. n.

urn:lsid:zoobank.org:act:30252D40-A093-48F8-9756-96A56C848B70

Type species: *Flagellobolus pauliani* sp. n., monotypic

Diagnosis: anterior and posterior gonopods of unique shape (Figs 23C, D): anterior gonopod with a telopodite process, retrorse part slender, located at midpoint of process instead of apically, a feature not shared with any other genus from Madagascar (Fig. 23D). Most unusual feature of *Flagellobolus* gen. n. is the unique elongation of the posterior gonopod telopodite into a simple, strongly elongated, thin tip (Figs

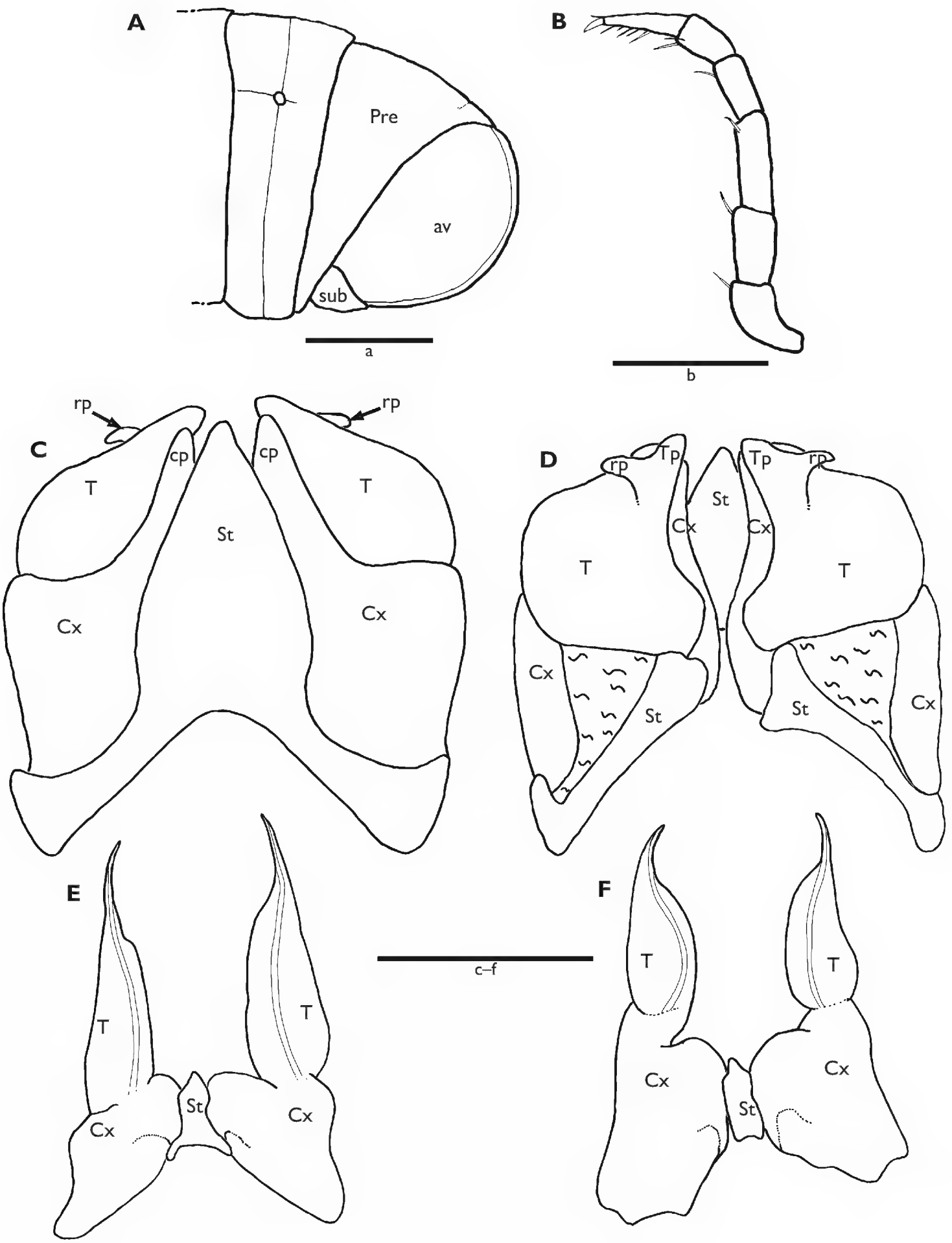


Figure 23. *Flagellobolus pauliani* sp. n., male holotype, **A** telson **B** left midbody leg **C** anterior gonopod, anterior view **D** anterior gonopod, posterior view **E** posterior gonopods, posterior view, slightly turned **F** posterior gonopods, posterior view, original position. av = anal valves; cp = coxite process; Cx = coxite; Pre = preanal ring; rp = retrorse process; St = sternite; sub = subanal scale; T = telopodite; Tp = telopodite process. Scale bars = 1 mm.

23E, F). This genus shares a small body size and elongated antennae with *Spiromimus*, *Zehntnerobolus*, *Alluviobolus* gen. n. and *Ostinobolus* gen. n. Gnathochilarium with a subdivided mentum and a single sclerotized ledge on each stipites, like in *Riotintobolus* gen. n., *Pseudocentrobolus* gen. n., *Granitobolus* gen. n., *Caprobolus* gen. n., *Alluviobolus* gen. n., *Ostinobolus* gen. n. Although the posterior gonopods of *Flagellobolus* gen. n. are connected by a large sternite, the telopodites do more closely resemble those of species of the Spirobolidea families Spirobolellidae and Pseudospirobolellidae instead of other Trigoniulidea.

Distribution and ecology: *Flagellobolus* was collected on Madagascar in the eastern rainforest of Périnet (Andasibe) and the montane rainforest of Andranomay. Its ecology is entirely unknown.

Etymology: *Flagellobolus*, masculine, is composed of '*flagello*', after *flagellum*, latin for whip, which refers to the characteristically shaped posterior gonopods, and *-bolus*.

***Flagellobolus pauliani* Wesener, sp. n.**
urn:lsid:zoobank.org:act:ADC7576D-F0BB-4D2B-B29C-23EFBA8679A3

Material examined: 2 ♂ *Holotype:* 1 ♂ (31 mm long), MNHN NoNumber, Madagascar, Périnet, rainforest, 18°57' S, 048°26' E, leg. R. Paulian, 20.XII.1955, IRSM.

Other material examined: 1 ♂, 1 imm., CASENT 9032806, Province d'Antananarivo, 3 km 41°NE Andranomay, 11.5 km 147°SSE Anjozorobe, montane rainforest, 1300 m, 18°28'24" S, 47°57'36" E, leg. Fisher, Griswold et al., pitfall traps, 5–13.XII.2000

Description. *Measurements*: male holotype with 42 body rings, circa 31 mm long, 2.4 mm wide.

Coloration almost completely decolorized because of alcohol, light stripe visible dorsally.

Head: each eye with circa 30 ocelli arranged in 5 or 6 vertical rows. Labrum with standard three irregular teeth and a single row of 10–12 stout marginal setae. Clypeus with two setiferous foveolae on each side. Antennal cavity absent. Antennae very long, protruding back to ring 7. Relative lengths of antennomeres: 1<2>3=4=5=6, antennomere 2 longest. Terminal antennomere with four large sensory cones located together inside a membranous area. Antennomere 5 latero-apically four or five rows, antennomere 6 with two or three rows of sensilla basiconica.

Gnathochilarium: lamellae linguales each with two standard setae located behind one another. Stipites each with three apical setae. Mentum basally subdivided by a prominent suture. *Mandible* not dissected.

Collum: smooth, laterally not protruding as far as ring 2.

Body rings: mostly smooth, with some irregular punctation on mesozona. Ozopores starting at ring 6, touching suture between mesozona and metazona. Ozopore on ring 6 located more ventrally than subsequent ozopores.

Telson: anal valves with weakly developed lips, with neither grooves, nor setae (Fig. 23A). Preanal ring and subanal process well-rounded, not extending beyond anal valves.

Legs: coxae 1 and 2 elongated and fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae. Length of midbody legs as long as body diameter in males. Each podomere with a single or pair of apical, ventral seta(e). Coxae 3 and beyond of cylindrical shape (Fig. 23B). Tarsus with a stout dorso-apical setae and three pairs of setae; apical pair stout, others successively much smaller.

Male sexual characters: tarsal pads absent (Fig. 23B). Coxae 3 and 4 each with a short, conical process. Process protruding posteriorly, but never overlapping adjacent coxa.

Anterior gonopod sternite elongated into a wide, triangular lobe with a well-rounded tip (Fig. 23C). Mesal process of coxite wide, long and well-rounded, shorter than sternite lobe (Fig. 23C). Process of telopodite large and slender, retrorse part not located apically, but basally of process (Fig. 23D). Retrorse projection slender, short with a well-rounded tip (Fig. 23D). *Posterior gonopods* unique (Figs 23E, F). Gonopod pair connected via a large, well-sclerotized sternite (Fig. 23E). Telopodites positioned parallel to one another. Coxite and telopodite not separated from one another, but dividing suture well-visible (Fig. 23E). Coxite wide, with a single groove and no appendage (Fig. 23F). Telopodite completely elongated into a process, apically tapering (Fig. 23F), very slender. Sperm canal running along mesal margin of telopodite, apically occupying whole width of joint (Fig. 23F).

Etymology: *pauliani,* adjective, after the collector Dr. Renaud Paulian (1913–2003), who collected numerous interesting millipedes on Madagascar.

Riotintobolus Wesener, gen. n.

urn:lsid:zoobank.org:act:2D3A99A5-E680-4E8D-BFD4-B10BD240636D

Type species: *Riotintobolus mandenensis* sp. n.

Other species included:
R. minutus sp. n.
R. aridus sp. n.
R. anomalus sp. n.

Diagnosis: only Malagasy Spirobolida genus where males in some species still have apodous rings in front of the telson. Body rings dorsally with a very wide stripe of flashy colour (Figs 24A, 40A), a unique feature, although slim stripes occur in several genera of Spirobolida. The posterior gonopods differ from other Spirobolida in the presence of a unique, finger-shaped process located laterally on the telopodite (Fig. 26M, x, y), and the presence of a large, very thin membrane located apically like a flag (Fig. 26M, z). Anal valves with extraordinary thick lips (absent in *R. anomalus* sp. n., Figs 26B, 27G), a unique character for this genus. Living specimens of *Riotintobolus mandenensis* sp. n. and *R. minu-*

tus sp. n. often remain stiff like a stick instead of rolling into a spiral when disturbed, a unique behaviour for Spirobolida. Telson with a well-developed, sharp-edged preanal process (absent in *R. anomalus* sp. n., Figs 26B, 27G, 28A), a feature only shared with *Pseudocentrobolus* gen. n. and *Granitobolus* gen. n. Collum not greatly enlarged, similar to *Spiromimus* and other small-bodied genera of Spirobolida. Gnathochilarium with a subdivided mentum and a single sclerotized ledge on each stipites (Figs 26F, G, 27C), like in *Flagellobolus*, *Pseudocentrobolus* gen. n., *Granitobolus* gen. n., *Caprobolus* gen. n., *Alluviobo-*

Figure 24. A *Riotintobolus mandenensis* sp. n., living specimens **B** pseudosteppe and burned shrubs dominating the area between the littoral forests of Mandena and Sainte Luce, SE Madagascar **C** Sainte Luce littoral forest, manioc plantation and destroyed trees inside conservation zone S8.

lus gen. n., *Ostinobolus* gen. n. Vulva simple, bivalve-like, similar to all other small-bodied genera of Spirobolida from Madagascar. Posterior plate apically overlapping anterior one. Anterior gonopods of a very general shape (Fig. 26K), similar to those of numerous other, probably not closely related genera, like *Aphistogoniulus* Silvestri, 1897 (Wesener et al. in press). Telopodite of posterior gonopod with a torsion: the sperm canal runs basally along the mesal margin, but is apically rotated, so that the opening is located at the lateral margin (Fig. 26M). A torsion also exists in *Zehntnerobolus* and *Alluviobolus* gen. n.

Distribution and ecology: two species, *Riotintobolus mandenensis* sp. n. and *R. minutus* sp. n. were collected in the littoral rainforest. The two other species occur in the spiny forest. *R. aridus* sp. n. was recorded from the spiny forest of Angavo, circa 20 km East of Antanimora, as well as Antafoky (Fig. 25), while *R. anomalus* sp. n. is recorded from the driest parts of Madagascar (Battistini 1972, Moat & Smith 2007), the Mahafaly plateau and the Cap Sainte Marie (Fig. 25). The genus *Riotintobolus* is the first example of a relationship between spiny forest and littoral rainforest species (Fig. 25). *R. mandenensis* sp. n. and *R. minutus* sp. n. are microendemic, *R. mandenensis* is most probably restricted to the littoral rainforest of Mandena, while *R. minutus* could only be found in Sainte Luce (Fig. 25). Both species from the littoral forest were collected inside the wet leaf litter, mainly on the bottom of the thin layer of leaves slightly above the root horizon. In both species the eyes are partly reduced, featuring only 12–20 fused ocelli (Figs 26A, C, 27E). Legs are also shorter than in the other two congeneric species (reaching only 0.7 times the diameter of body rings, Fig. 27D). No explanation can be given for the unique and highly unusual defence behaviour of *R. mandenensis* and *R. minutus*. Both species turn stiff and motionless like a stick and rarely curl into a spiral like most other species of the Spirobolida.

Description. *Males*: length up to 45 mm, diameter up to 4.3 mm. 38–45 podous and up to two additional apodous rings. Females: length up to 51 mm, diameter up to 4.6 mm. 39–45 podous and up to two additional apodous rings.

Colour highly species-specific, ventrally always with a distinct wide stripe, see species for accurate descriptions.

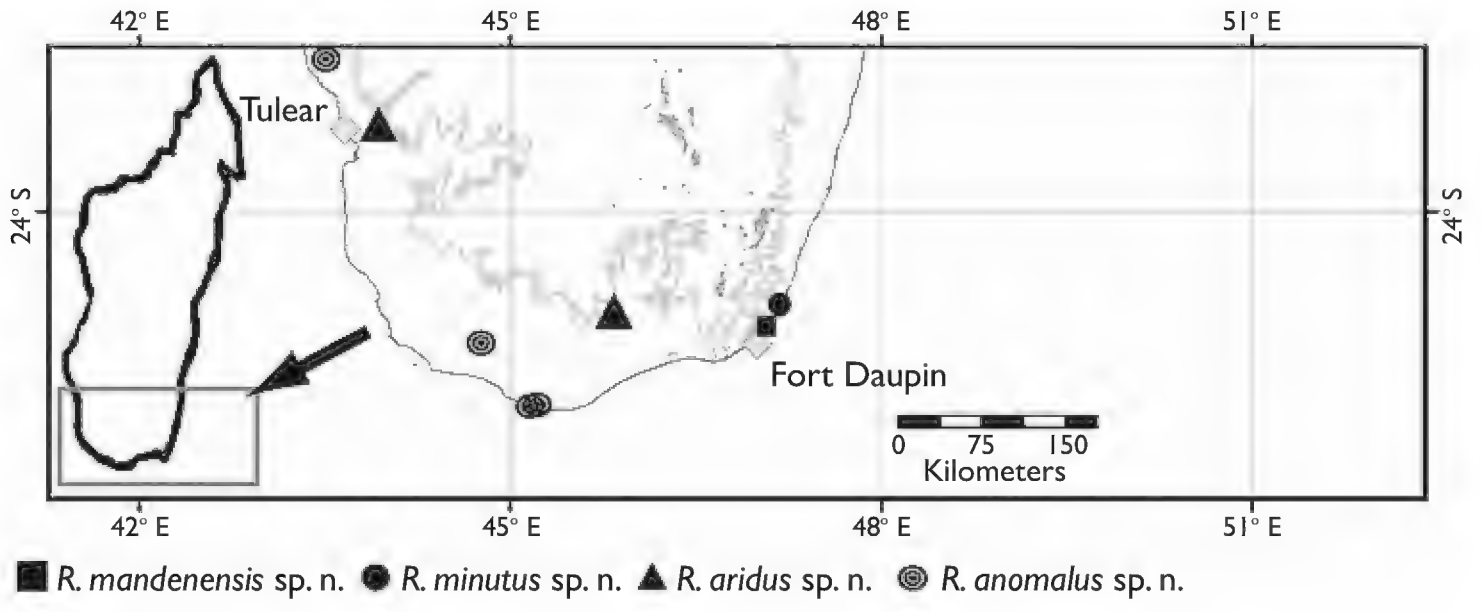


Figure 25. Distribution of the genus *Riotintobolus* gen. n.

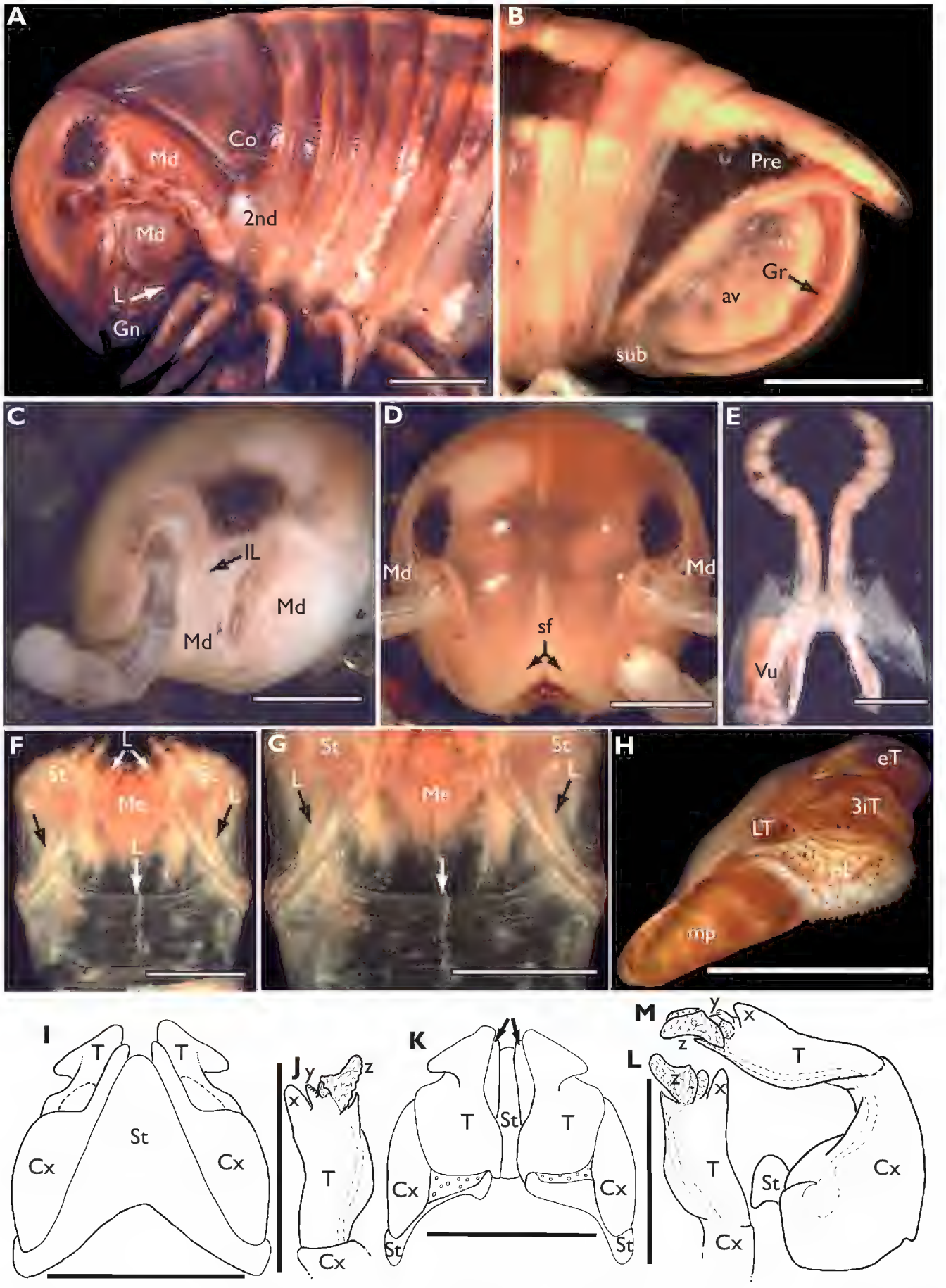


Figure 26. *Riotintobolus mandenensis* sp. n., A, B, I–M male holotype, C–H female paratype. **A** head, lateral view **B** telson **C** head, detail of incisura lateralis **D** head, frontal view **E** second leg with vulva **F** gnathochilarium, overview **G** gnathochilarium, detail of mentum **H** left mandible, mesal view **I** anterior gonopod, anterior view **J** left posterior gonopod, anterior view **K** anterior gonopod, posterior view **L** telopodite of left posterior gonopod, posterior view **M** left posterior gonopod, overview, posterior view. 3iT = 3-combed internal tooth; av = anal valves; Co = collum; Cx = coxite; eT = external tooth; Gn = gnathochilarium; Gr = groove; IL = incisura lateralis; L = ledge; LL = lamella linguales; LT = lateral tooth; Md = mandible; Me = mentum; mp = molar plate; pL = pectinate lamella; Pre = preanal ring; sf = setiferous foveolae; St = sternite; ST = stipites; sub = subanal scale; T = telopodite; Vu = vulva. Scale bars = 1 mm.

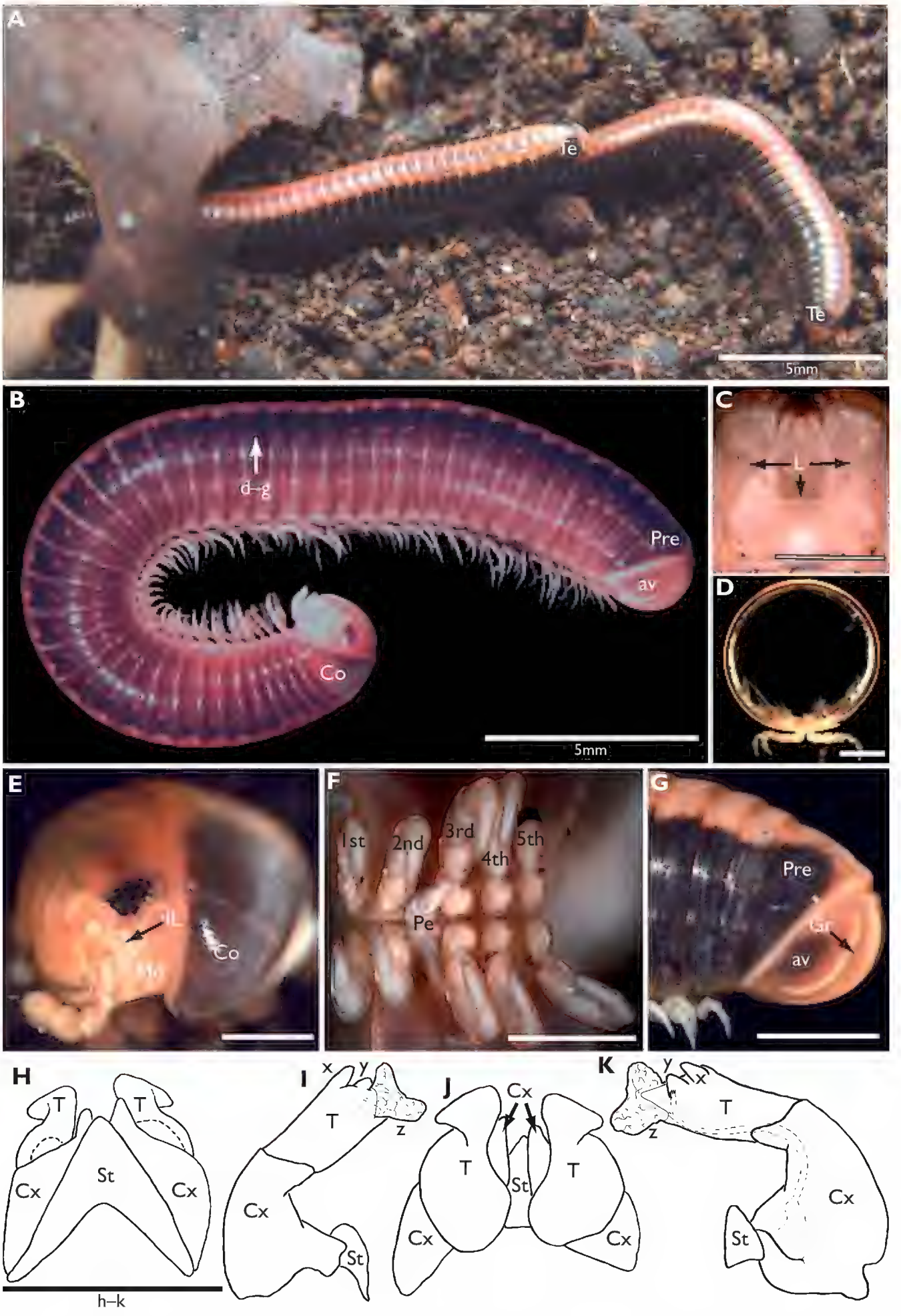


Figure 27. *Riotintobolus minutus* sp. n., **A–E** female paratype(s), **F–K** male holotype. **A** two living specimens **B** habitus **C** gnathochilarium, overview; **D** midbody ring with leg pair **E** head, detail of incisura lateralis **F** legs 1–5, ventral view **G** telson **H** anterior gonopod, anterior view **I** left posterior gonopod, anterior view **J** anterior gonopod, posterior view **K** left posterior gonopod, posterior view. av = anal valves; Co = collum; Cx = coxite; d-g = ozopores; Gr = groove; IL = incisura lateralis; L = ledge; Md = mandible; Pe = "penes"; Pre = preanal ring; St = sternite; T = telopodite; Te = telson. Scale bars = 1 mm.

Head: each eye either with circa 28–34 (*R. aridus* and *R. anomalus*), or 12–20 (*R. mandenensis* and *R. minutus*) partly fused ocelli arranged in 3–5 vertical rows (Figs 26C, 27E). Labrum with standard three irregular teeth and a row of 10–12 stout marginal setae. Clypeus with two (rarely three) setiferous foveolae on each side (Fig. 26D). Antennae short or of medium length, reaching back to ring 2 or 5 (Figs 26A, 27B). Relative lengths of antennomeres: 1<<2>3=4=5<6 (Figs 26A, 28B, 29B). Terminal antennomere with four large sensory cones located together inside a membranous area. Antennomere 5 latero-apically with a field of four rows, antennomere 6 with a field of two rows of sensilla basiconica.

Gnathochilarium unusual (Fig. 26F). Lamellae linguales each with two standard setae located behind one another. Stipites each with three apical setae (Fig. 26F). Mentum basally subdivided by a wide suture (Figs 26G, 27C). Stipites each towards mentum with a large sclerotized ledge (Fig. 26G) Palpi of gnathochilarium with numerous sensilla. Hypopharyngeal crest with a field of spine-like structures. Central pads of endochilarium separated by a step into two levels, each carrying sensory cones, number of cones not counted.

Mandible: external tooth simple, rounded; mesal tooth with three shallow cusps (Fig. 26H). Four or five pectinate lamellae. Molar plate with few (five) transverse furrows, anterior two furrows enlarged, posterior furrows minute.

Collum: smooth, laterally not protruding as far as ring 2 (Fig. 26A).

Body rings: dorsally and laterally smooth, meso- and metazona ventrally with numerous transverse impressions. Ozopores starting at ring 6, touching suture between mesozona and metazona (Fig. 27B).

Telson: preanal process protruding, sharp-edged (except for *R. anomalus* sp. n.). Anal valves with well-visible lips and micropunctation (Fig. 26B). Deep groove present anteriorly to sharp-edged lips in *R. mandenensis* sp. n. and *R. minutus* sp. n. (Figs 26B, 27G).

Legs: coxae 1 and 2 elongated and fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae. Length of midbody legs species-specific (Figs 27D, 28C, 29C). Each podomere with an apical ventral seta. Coxae 3 and beyond of cylindrical shape (Figs 28C, 29C). Tarsus with a stout dorso-apical seta and three pairs of ventral setae. Tibia short, half as long as tarsus (Figs 28C, 29C).

Male sexual characters: male legs in some species with tarsal pads. Male coxae 3–7 unmodified (Fig. 27F).

Anterior gonopods: median sternal projection triangular, broadly rounded (Fig. 26I). Sternite longer than coxite, but slightly shorter than mesal process of coxite (Fig. 26I). Process of coxite long, but shorter than telopodite (Fig. 26I). Telopodite always with a large, triangular retrorse process. Retrorse process laterally and apically extending beyond telopodite and coxite (Fig. 26K).

Posterior gonopods coxite and telopodite clearly separated (Figs 26J, M). Sternite sclerotized and well-visible (Fig. 26M). Coxite mesally with a single groove, coxite protruding into a short stem towards telopodite. Telopodite slightly shorter than coxite (Fig. 26M). Sperm canal discharging apically and laterally instead of mesally because of a torsion (Figs 26J, M). Telopodites laterally always with a finger-shaped process (Fig. 26M, x, y), apically with a large, thin membrane (Fig. 26M,

z). Width of membrane apically larger than basally. Sperm canal first running along inner margin of coxite and sternite, than apically running through the telopodite before discharging laterally on finger-shaped process and often also apically into thin membrane (Fig. 26M).

Female sexual characters: vulva simple, with a small, poorly sclerotized operculum at base, bivalve-like. Posterior valve apically overlapping anterior valve. Both valves smooth, lacking sensory cones. Towards opening basally on each valve with two or three rows of setae.

Etymology: *Riotintobolus*, masculine, refers to the mining company Rio Tinto®. Rio Tinto's subsidiary, Qit Madgascar Minearls®, now owns the littoral rainforests of Mandena and Sainte Luce (Vincelette et al. 2003). This encompasses all the remaining distribution area of *Riotintobolus mandenensis* sp. n., which only occurs in Mandena, and of *R. minutus* sp. n., a species only recorded from Sainte Luce. Conservation zones will be the only remaining natural habitat after a large-scale mining action is undertaken by Riotinto in the coming years (Ganzhorn et al. 2003, Bollen and Donati 2006). These conservation zones will be directly managed by Qit Madagascar Minerals in order to conserve the biodiversity of the forests. The proposed conservation zones are 160 ha (but divided by a swamp) for the littoral forest of Mandena, and *Riotintobolus mandenensis* sp. n. The conservation zone for *R. minutus* sp. n., the S9 fragment of Sainte Luce is circa 200 ha large. The area between both forests is already degraded to pseudosteppe (Fig. 24B). The conservation zones, at least of the Sainte Luce fragment, are still under human pressure (Fig. 24C). Since Rio Tinto® owns and is responsible for the only remaining habitat where two *Riotintobolus* **gen. n.** species exist, the whole genus is named after the company. The author hopes that this move will increase the probability of the survival of *R. mandenensis* sp. n. and *R. minutus* sp. n.

Key to the *Riotintobolus* species:

1 Tarsal pads absent (Fig. 27F). Eyes with 20 or less ocelli (Figs 26A, 27E). Anal valves with a deep groove between anterior half and sharp-edged lips (Figs 26B, 27G) **2**

– At least male legs 3–7 with tarsal pads (Fig. 29C). Eyes with more than 25 ocelli. Anal valves with neither a groove, nor sharp-edged lips (Figs 28A, 29A) **3**

2 Specimens 35–43 mm long. Colour laterally black, dorsally with a thick, light brown stripe (Fig. 24A). Telopodite of posterior gonopod laterally with one large and second small finger-shaped process (Fig. 26M)..... ***R. mandenensis* sp. n.**

– Specimens shorter than 25 mm. Colour laterally black, dorsally with a thick, red stripe (Fig. 27A). Telopodite of posterior gonopod laterally with two large finger-shaped processes of equal size (Fig. 27K)..... ***R. minutus* sp. n.**

3 Telson with an elongated, protruding preanal process, lips on anal valves well-developed (Fig. 28A). Only male legs 3–7 with tarsal pads. Apical mem-

brane on posterior gonopod weakly developed (Fig. 28G). Telopodite at mesal margin with a suspicious horn (Fig. 28F). Colour brown-blackish with a conspicuously wide light brown stripe.....***R. aridus* sp. n.**

– Telson preanal process not protruding, lips on anal valves weakly developed (Fig. 29A). Male legs three and beyond with tarsal pads (Fig. 29C). Apical membrane on posterior gonopod large, widely protruding (Fig. 29F). Colour light grey, posterior margin of rings dark grey, dorsally with a conspicuous, wide blood-red stripe ..... ***R. anomalus* sp. n.**

***Riotintobolus mandenensis* Wesener, sp. n.**
urn:lsid:zoobank.org:act:7C0503C7-C70F-4FA4-A9A8-4E9F049E5391

Material examined: 1 ♂, 16 ♀, 20 imm. *Holotype:* 1 ♂ (36 mm long, dissected), FMMC W040C, Province Toliara, Mandena, littoral forest on sand, 34 m, 24°57.260' S, 46°59.499' E, leg. T. Wesener et al., 02.VI.2007. *Paratypes:* 5 ♀, 5 imm., FMMC W039C, same data as holotype; 1 ♀, 2 imm., CAS W039C, same data as holotype; 1 ♀, 2 imm., ZMUC W39C, same data as holotype; 1 ♀, 2 imm., ZMH W39C, same data as holotype; 1 ♀, 2 imm., ZSM W039C, same data as holotype.

Other material examined: 7 ♀, 7 imm., **W039C**, same data as holotype, University Antananarivo.

Differential diagnosis: the size and special colour pattern are unique for Malagasy millipedes. The gonopods of this species are similar in some aspects to those of *R. minutus* sp. n. and *R. anomalus* sp. n., but the posterior gonopods are of a unique shape.

Description. *Measurements*: holotype with 41 podous and 2 apodous rings, 36 mm long, 3.1 mm wide. Females with 41–43 podous and 0–2 apodous body rings, 37–43 mm long, 4.2–4.4 mm wide.

Coloration black, dorsally with an extraordinary wide, light brown stripe (Fig. 24A). Posterior half of collum dorsally black (Fig. 26A). Head, legs and antennae light brown. *Eyes* with 16–20 almost fused ocelli arranged in 4 or 5 rows (Figs 26A, C). *Antennae* protruding back to body ring 2 (Fig. 26A). *Legs* without tarsal pads. Male legs reach 0.7 times, female legs 0.6 times body diameter. *Preanal process* sharp-edged, straight, protruding above anal valves (Fig. 26B). Anal valves small, between anterior part and lips with a deep groove, margin towards groove sharp-edged (Fig. 26B).

Anterior gonopod sternite basally wide, apically elevated into a lobe with a triangular, well-rounded tip (Fig. 26I). Sternite tip almost as high as mesal process of coxite; latter relatively slender, elongated, longer than sternite (Fig. 26I). Telopodite on posterior side apically with a large triangular, retrorse process (Fig. 26K). Process projecting above coxite and telopodite (Fig. 26K).

Posterior gonopods telopodite laterally with a single, large, finger-shaped process (Fig. 26J, x). Second small projection, where sperm canal is discharging, is located close to apex (Fig. 26M, y). A large, bi-lobical membrane present apically. Membrane

apically three times wider than basally (Fig. 26L, z). A small, white, swollen area (Fig. 26M) is also located basally of membrane.

Intraspecific variation: females exist in different size classes. The presence of apodous rings in front of the telson in mature specimens hint to the existence of post-maturity moults.

Distribution and ecology: this species was only collected in the littoral rainforest on sand of Mandena (Fig. 25). Only 160 ha of this forest will remain after a large-scale mining project (Vincelette et al. 2003). All specimens were collected directly on the root layer under a thin layer of leaf litter. Disturbed specimens often did not curl into a spiral but remained motionless and stiff like a stick even when picked up. Because of their black/light-brown colour pattern (Fig. 24A), specimens of *R. mandenensis* were quite difficult to detect against the background consisting of sand with some darker top soil inclusion. The giant pill-millipede species *Sphaeromimus inexpectatus* Wesener & Sierwald, 2005 is also only known from a small area surrounding Mandena (Wesener and Sierwald 2005).

Etymology: *mandenensis*, adjective, refers to the only area where this species lives, the littoral forest of Mandena.

***Riotintobolus minutus* Wesener, sp. n.**

urn:lsid:zoobank.org:act:69657A54-E55E-4B78-BD6A-C14D398BC1F6

Material examined: 1 ♂, 2 ♀, 2 imm. *Holotype:* 1 ♂ (22 mm long), FMMC, Province Toliara, Sainte Luce, S9, littoral forest on sand, in leaf litter (deep), 24°47' S, 47°10' E, leg. T. Wesener, 06.IV.2003. *Paratypes:* 1 ♀, 2 imm., FMMC, same data as holotype; 1 ♀, FMMC W031B, Sainte Luce, S9, in leaf litter with roots, 24°46.769' S, 47°10.288' E, 12 m, littoral forest on sand, leg. Wesener et al., 01.VI.2007.

Differential diagnosis: *R. minutus* is the smallest known species of the genus and with a body length in mature males of only 22 mm, one of the smallest Spirobolida species known from Madagascar. The pitch-black colour with a thick dorsal red stripe (Fig. 27A) helps to clearly identify this species. The gonopods of this species are in some aspects similar to those of *R. mandenensis* and *R. anomalus* sp. n.

Description. *Measurements*: male holotype with 38 podous and 2 apodous rings, 22 mm long, 2.3 mm wide. Females with 39–41 podous and 0–2 apodous body rings, 23–26 mm long, 2.9 mm wide.

Coloration pitch-black, dorsally with an extraordinary wide, red stripe (Fig. 27A). Openings of ozopores highlighted by a red spot (Fig. 27B). Posterior half of collum dorsally black (Fig. 27E). Head, lateral part of anal valves and subanal scale red, legs whitish brown (Fig.40B). *Eyes* with 12–14 partly fused ocelli arranged in three rows (Fig. 27E). *Antennae* protruding back to body ring 2 (Fig. 27B). *Legs* lacking tarsal pads. Male legs reach 0.7 times, female legs 0.5 times, body diameter (Fig. 27D). *Preanal process* sharp-edged, but not protruding above anal valves (Fig. 27G). Anal valves small, at mid-anterior part with a deep groove. Margin of lip towards groove sharp-edged (Fig. 27G).

Anterior gonopod sternite apically elevated into a wide lobe with a triangular, well-rounded tip (Fig. 27H). Sternite tip almost as high as mesal coxite process, which is relatively slender but longer than sternite (Fig. 27H). Telopodite on posterior side apically with a large triangular, retrorse process (Fig. 27J), which is projecting above coxite and telopodite margins (Fig. 27J).

Posterior gonopods telopodite laterally with two large, finger-shaped processes (Fig. 27I). Sperm canal discharging at more apical process. Apically, a large membrane present, extending into two lobes, apically twice as wide as basally (Fig. 27K).

Intraspecific variation: females with 39+2 and 41+0 body rings are known, indicating post-mature moults.

Distribution and ecology: this species was only collected in the isolated littoral rainforest on sand in Sainte Luce (Fig. 25). Only circa 200 ha of this forest will remain after a large scale mining project (Vincelette et al. 2003, Bollen and Donati 2006). Although officially protected, large scale wood removal and even slash-and-burn agriculture (Fig. 24C) is still ongoing in this forest (own observations in March 2003 and June 2007). The surrounding pseudosteppe is regularly burned, further endangering this forest (Fig. 24B). However, further searches should be conducted in small remaining coastal forests north of Sainte Luce, where this species could also occur. All specimens were found deep in the soil under the wet leaf litter. Disturbed specimens often did not curl into a spiral, but remained motionless and stiff like a stick even when picked up. The giant pill-millipede species *Sphaeromimus splendidus* Wesener & Sierwald, 2005 and a still undescribed *Zoosphaerium* species are currently also only known from the littoral forest of Sainte Luce (Wesener and Sierwald 2005, Wesener and Wägele 2008).

Etymology: *minutus*, adjective, refers to the small size of this species.

Riotintobolus aridus Wesener, sp. n.

urn:lsid:zoobank.org:act:835C43EF-EB42-4673-8C10-60DBEE26A533

Material examined: *Holotype:* ♂ (30 mm long), MNHN, Province Toliara, Angavo, à l'est d'Antanimora, probably spiny forest, 24°50'57" S, 45°48'6" E, leg. R. Decary, "sous des pierres", 19.VI.1927, entrée 17–1927.

Other material examined: 2 ♂, 1 ♀, 10 imm., CASENT 9032799, Province Toliara, Antafiky, gallery forest, 50 m, 23°28'23" S, 44°4'19" E, leg. Frontier Project, millipede dig (3 m x 3 m), 10.X.2001; 2 ♀, 10 imm., CAS MGF009, Province Toliara, Antafiky, gallery forest, 50 m, 23°29'16" S, 44°4'39" E, leg. Frontier Project, millipede dig (3 m x 3 m), 22.VII.2001; 2 ♀, CAS MGF012, Province Toliara, Antafiky, spiny forest thicket, 150 m, 23°28'24" S, 44°4'23" E, leg. Frontier Project, millipede dig (3 m x 3 m), 30.VII.2001; 10 imm., CAS MGF010, Province Toliara, Antafiky, gallery forest, 70 m, 23°28'45" S, 44°3'59" E, leg. Frontier Project, millipede dig (3m x 3m), 13.X.2001; 6 imm., CAS MGF007, Province Toliara, Antafiky, spiny forest thicket, 80 m, 23°29'16" S, 44°4'39" E, leg. Frontier Project, millipede dig (3 m x 3 m), 14.XI.2001.

Differential diagnosis: *R. aridus* has special shaped posterior gonopods, featuring a horn-like process, which is unique and aids in the identification of this species.

Description. *Measurements*: male holotype with 44 podous and no apodous rings, circa 30 mm long (broken), 2.6 mm wide.

Coloration at legs light brown, ventrally light brown, dorsolaterally dark brown to black, dorsally with a wide light brown stripe, middle of stripe with a row of black spots located anteriorly on each body ring. Colour altogether similar to *R. mandenensis*.

Eyes with 27 or 28 ocelli arranged in five rows.

Antennae protruding back to body ring 2 (Fig. 28B). *Legs* 3–7 in males with tarsal pads. Male legs reach 0.9 times body diameter (Fig. 28C). *Preanal process* sharp-edged, protruding above anal valves (Fig. 28A). Anal valves small, with well-developed lips, groove absent (Fig. 28A).

Anterior gonopod sternite apically elevated into a wide lobe with a triangular, well-rounded tip (Fig. 28D), almost as high as long mesal coxite process, latter relatively slender, slightly longer than sternite (Fig. 28D). Telopodite on posterior side apically with a large triangular, retrorse process (Fig. 28E), which projects above coxite and telopodite (Fig. 28E).

Posterior gonopods telopodite laterally with two large, finger-shaped processes (Fig. 28F). Sperm canal discharging into apical-most process, opening of sperm duct visible in anterior view (Fig. 28F). Apically, a large membrane present, not extending into lobes- membrane apically as wide as basally (Fig. 28G). Telopodite at mesal margin basally of membrane with a slender, long horn (Fig. 28G). In anterior view between horn and membrane with an additional, small finger-shaped process (Fig. 28F).

Distribution and ecology: the type specimen collected by R. Decary more than 80 years ago states on the collection label "Angavo, á l'est d'Antanimora". On Madagascar several places with the name "Angavo" exist, as well as some populated places called Antanimora. However, only a single locality called Angavo is located east of Antanimora. This locality is a hilly area inside the spiny forest region of southern

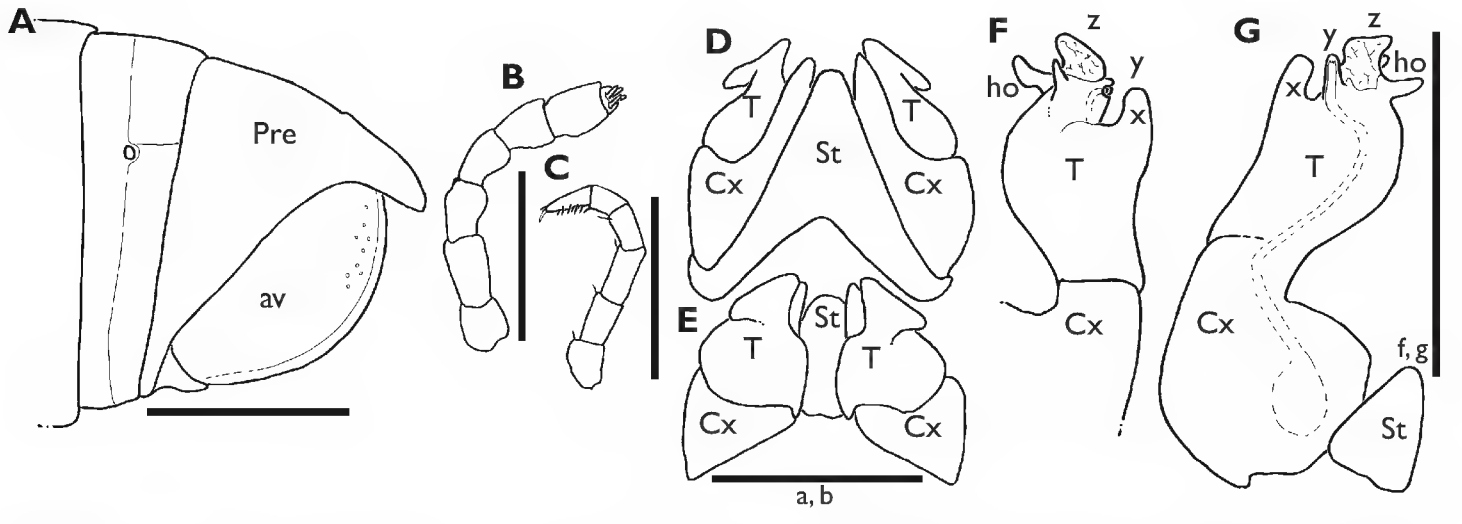


Figure 28. *Riotintobolus aridus* sp. n., male holotype, **A** telson **B** left antenna **C** left midbody leg **D** anterior gonopod, anterior view **E** anterior gonopod, posterior view **F** posterior gonopods, anterior view **G** posterior gonopods, posterior view. av = anal valves; Cx = coxite; ho = horn; Md = mandible; Pre = preanal ring; St = sternite; T = telopodite. Scale bars = 1 mm.

Madagascar (Fig. 25), and was traced using a recent map (Moat and Smith 2007). The collection label indicates that the single known specimen of *R. aridus* was found under a stone. Additional specimens were recently collected circa 250 km east at Antafoky.

Etymology: *aridus*, adjective, refers to type locality of this species, which is located in one of the driest parts of Madagascar.

Riotintobolus anomalus Wesener, sp. n.

urn:lsid:zoobank.org:act:D393DC52-5565-41B3-BA6E-D8ED7FAE46BA

Material examined: *Holotype:* 1 ♂ (45 mm long), CAS BLF 5499, Madagascar, Province Toliara, Réserve Spéciale de Cap Sainte Marie, 12.3 km 262°W Marovato, spiny forest thicket, 200 m, 25°34'54" S, 45°10'6" E, leg. Fisher, Griswold et al., pitfall trap, 11–15.II.2002. *Paratypes:* >25 ♂ and ♀, CAS BLF 5499, same data as previous; 2 ♂, 3 ♀, CAS BLF 5651, same data as previous, but 160 m, 25°35'40" S, 45°8'49" E, leg. Fisher, Griswold et al., malaise trap, 13–19.II.2002.

Other material examined: 1 ♀, CAS BLF 5503, Réserve Spéciale de Cap Sainte Marie, spiny forest thicket, 200 m, 25°34'54" S, 45°10'6" E, leg. Fisher, Griswold, et al., 11–15.II.2002; 1 ♂, CAS BLF 5758, Madagascar, Province Toliara, Mahafaly Plateau, 6.2 km 74°ENE Itampolo, spiny forest thicket, 80 m, 24°39'13" S, 43°59'48" E, leg. Fisher, Griswold et al., sifted litter, 21–25.II.2002; 2 ♂, CAS BLF 5762, same data as previous, but hand collecting; 13 ♂, 6 ♀, CAS BLF 5763, same data as previous, but pitfall trap; 1 ♂, MNHN, Madagascar, leg. Petit, 24–1922, envoi vi, entrée 24–1922; 1 ♂, CASENT 9032805, Province Toliara, Lake Ranobe, spiny forest, 30 m, 23°2.941' S, 43°36.635' E, leg. Frontier Wilderness Project, 21–28.I.2003.

Differential diagnosis: *R. anomalus* is the only known species of *Riotintobolus* where a sharp-edged preanal process and well-developed lips are absent. Furthermore it is the only species with male tarsal pads on every leg pair. The gonopods of this species are distinct but in some aspects similar to those of *R. mandenensis* and *R. minutus*.

Description. *Measurements*: male holotype with 45 podous and no apodous rings, circa 45 mm long (broken), 4.3 mm wide. Females with 44 or 45 body rings and no apodous ring, up to 51 mm long, 4.6 mm wide.

Coloration light grey with darker posterior margins. Openings of ozopores highlighted with a black spot. Collum and rings dorsally with an extraordinary wide blood-red or rust-red stripe. Antennae and legs dark grey. *Eyes* with 30–34 ocelli arranged in five rows. *Antennae* short, protruding in both sexes back to body ring 2 (Fig. 29B). *Legs* reach 0.7 times body diameter, tarsi 3 and beyond in males with tarsal pads (Fig. 29C). *Preanal process* absent, not protruding (Fig. 29A). Anal valves small, lips weakly developed (Fig. 29A).

Anterior gonopod sternite apically swollen into a wide lobe with a triangular, well-rounded tip (Fig. 29D). Sternite tip almost as high as mesal coxite process, latter long, relatively slender, longer than sternite (Fig. 29D). Telopodite on posterior side apically

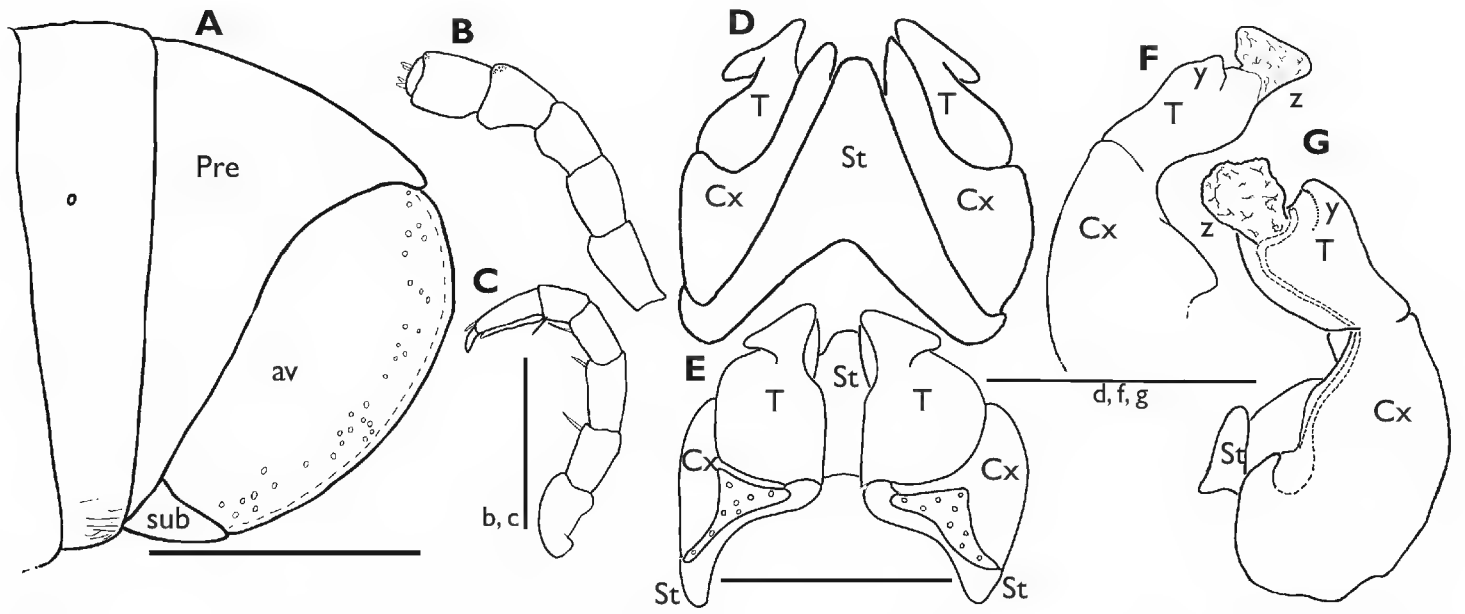


Figure 29. *Riotintobolus anomalus* sp. n., A–C, male (**MNHN**), D–G male holotype, **A** telson **B** right antenna **C** left midbody leg **D** anterior gonopod, anterior view **E** anterior gonopod, posterior view **F** posterior gonopods, anterior view **G** posterior gonopods, posterior view. av = anal valves; Cx = coxite; Md = mandible; Pre = preanal ring; St = sternite; sub = subanal scale; T = telopodite. Scale bars = 1 mm.

with a large triangular retrorse process (Fig. 29E), projecting above coxite and telopodite margins (Fig. 29E).

Posterior gonopods telopodite laterally with a single, large, finger-shaped process (Fig. 29F). Sperm canal discharging into process. Apically, a large membrane present, which extends into two lobes, apically twice as wide as basally (Fig. 29G).

Intraspecific variation: no variation inside or in between the Mahafaly and Cap Sainte Marie populations was observed.

Distribution and ecology: this species is currently known from the Mahafaly plateau, the Cap Sainte Marie, and a third, distant location at the Lake Ranobe. All localities are probably the driest places on Madagascar (Battistini 1972, Moat & Smith 2007).

Etymology: *anomalus*, adjective, refers to the unusual (for *Riotintobolus*) telson of the species.

***Pseudocentrobolus* Wesener, gen. n.**
urn:lsid:zoobank.org:act:4DFE0C0E-5992-4BCC-A6B4-557EC7B6FF65

Type species: *Pseudocentrobolus aureus* sp. n.

Other species included:
P. vohibasiensis sp. n.

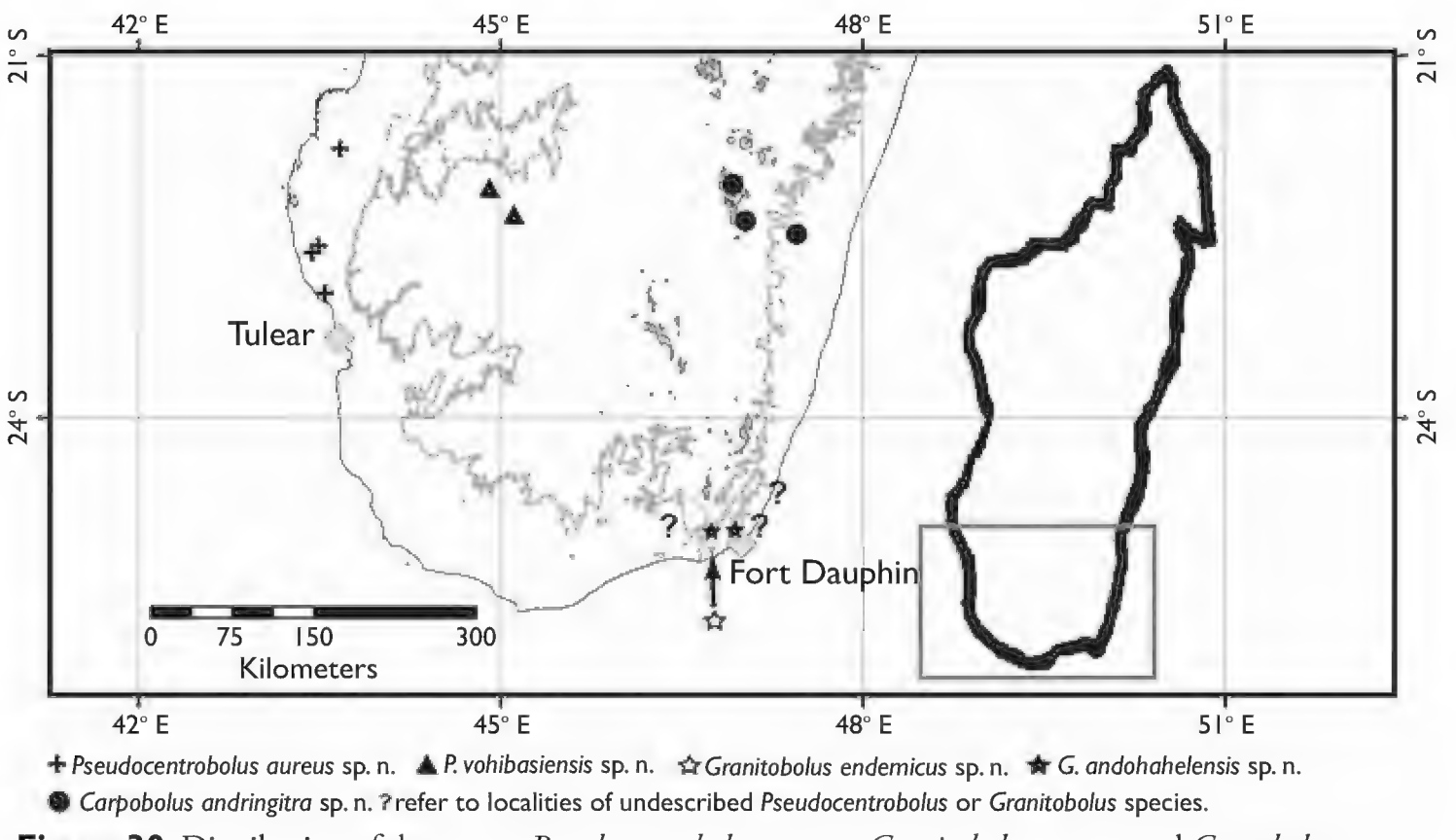
Diagnosis: posterior gonopods are unique, distinct (Figs 35C–F): telopodite basally with a membranous process carrying sperm canal; telopodite apically with a distinct, unique rounded disc, which is covered with numerous spine-like structures (Figs 35B,

E); coxite basally at sperm canal with an obligate finger-shaped process, which is not curved but straight like in *Granitobolus* gen. n. Natural coloration conspicuously contrasting, with golden, black or red pattern (Figs 31A, C, D, 36B). Gnathochilarium with a subdivided mentum and a single sclerotized ledge on each stipites (Figs 32D–F), like in *Flagellobolus*, *Riotintobolus*, *Granitobolus* gen. n., *Caprobolus* gen. n., *Alluviobolus* gen. n., *Ostinobolus* **gen. n**. Shares numerous characters only with species of the genus *Granitobolus* gen. n.: a stout preanal process, which prominently extends beyond anal valves (Figs 31C, 36B), well-developed lips on the anal valves, thick moniliform body rings which overlap each widely to the metazonite (Fig. 31C), rectangular extensions (Figs 33B, C) on the posterior margins of the rings and a greatly enlarged collum, which is ventrally longer than the body ring 2. The habitus and shape of the anterior gonopod (Figs 34A, B) are also very similar to species of *Granitobolus* gen. n.

Distribution and ecology: two species of *Pseudocentrobolus* are recorded from the dry spiny and subhumid forests in Southwestern Madagascar (Fig. 30). A third species, whose external characters fit very well into *Pseudocentrobolus* but where no mature male could be collected, was discovered in the spiny forest of Andohahela in Southeastern Madagascar (Fig. 30).

Description. *Males*: length up to 48 mm, diameter up to 4.5 mm. 38–40 podous rings. Females: length up to 48 mm, diameter up to 5.1 mm. 39 or 40 podous rings. Apodous rings absent in all adult specimens.

Colour (after short time in alcohol): mesozona golden (Fig. 31A) or greenish (faded to grey in some specimens), metazona blackish (Fig. 31A) or golden (Fig. 36B). Head, antennae, gonopods, legs and at least posterior part of telson golden (Fig. 31C) or reddish (Fig. 36B).


42° E
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+ Pseudocentrobolus aureus sp. n. ▲ P. vohibasiensis sp. n. ☆ Granitobolus endemicus sp. n. ★ G. andohahelensis sp. n.
● Carpobolus andringitra sp. n. ? refer to localities of undescribed Pseudocentrobolus or Granitobolus species.

Figure 30. Distribution of the genera *Pseudocentrobolus* gen. n., *Granitobolus* gen. n. and *Caprobolus* gen. n.

Head: each eye with circa 38–42 ocelli arranged in 7 or 8 vertical rows (Figs 31D, 36A). Labrum with standard three irregular teeth and one row of 10–12 stout marginal setae (Fig. 36A). Clypeus with two setiferous foveolae on each side. Antennae short or very short, reaching back to ring 2 or 4 (Figs 31D, 36A). Relative lengths of antennomeres: 1<2=3=4=5=6 (Fig. 32B). Terminal antennomere with four large sensory cones located together inside a membranous area (Fig. 32A). Antennomere 5 latero-apically with four rows, antennomere 6 with two rows (Figs 32A, C) of sensilla basiconica.

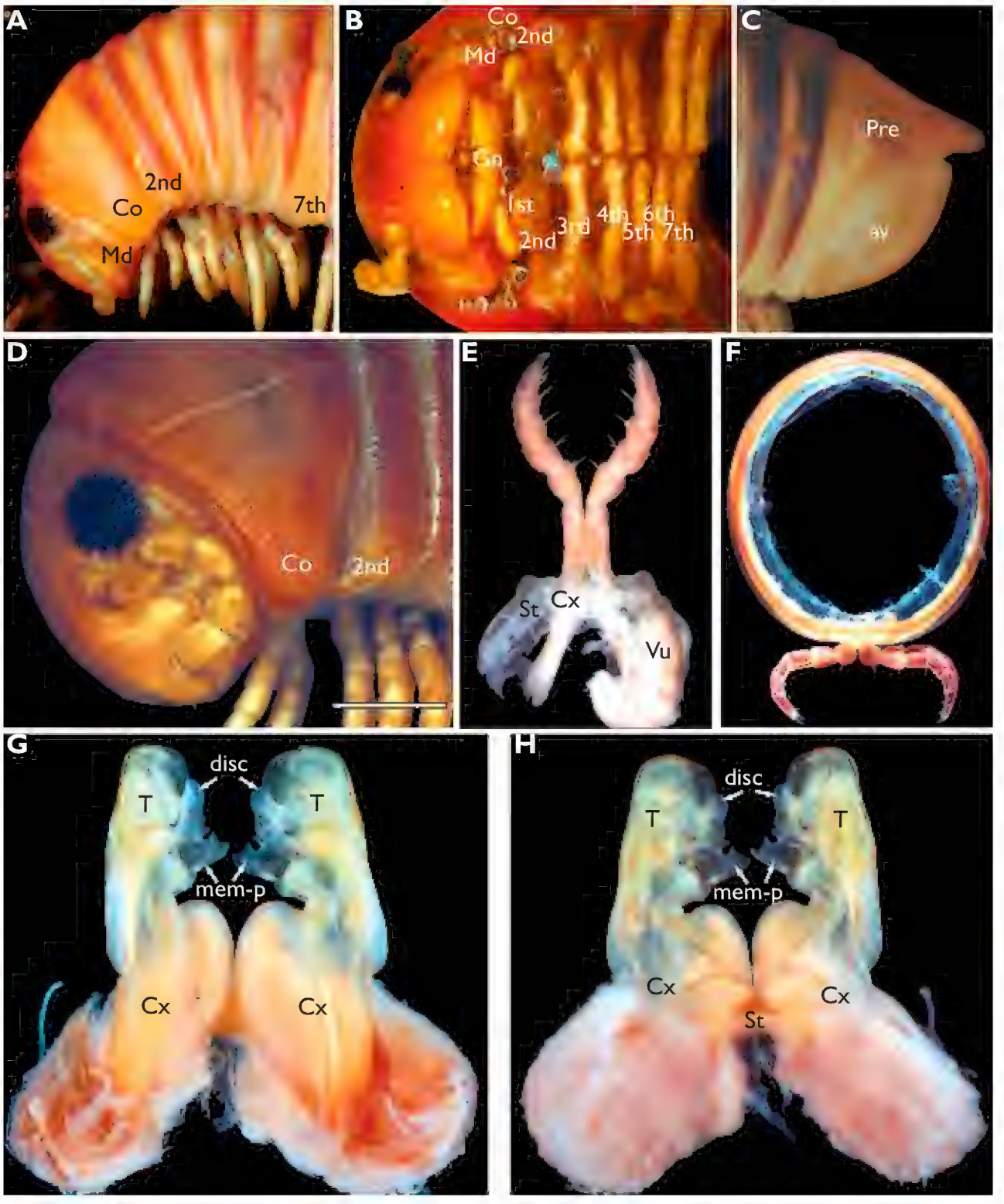

Figure 31. *Pseudocentrobolus aureus* sp. n., A–D, G, H male paratype; E, F female paratype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** head, antenna and collum, lateral view **E** second leg with vulva **F** female midbody ring with legs **G** posterior gonopods, anterior view **H** posterior gonopods, posterior view. av = anal valves; Co = collum; Cx = coxite; Gn = gnathochilarium; Md = mandible; mem-p = membranous process; Pre = preanal ring; St = sternite; St-Cx = coxosternite; T = telopodite; Vu = vulva. Scale bars = 1 mm.

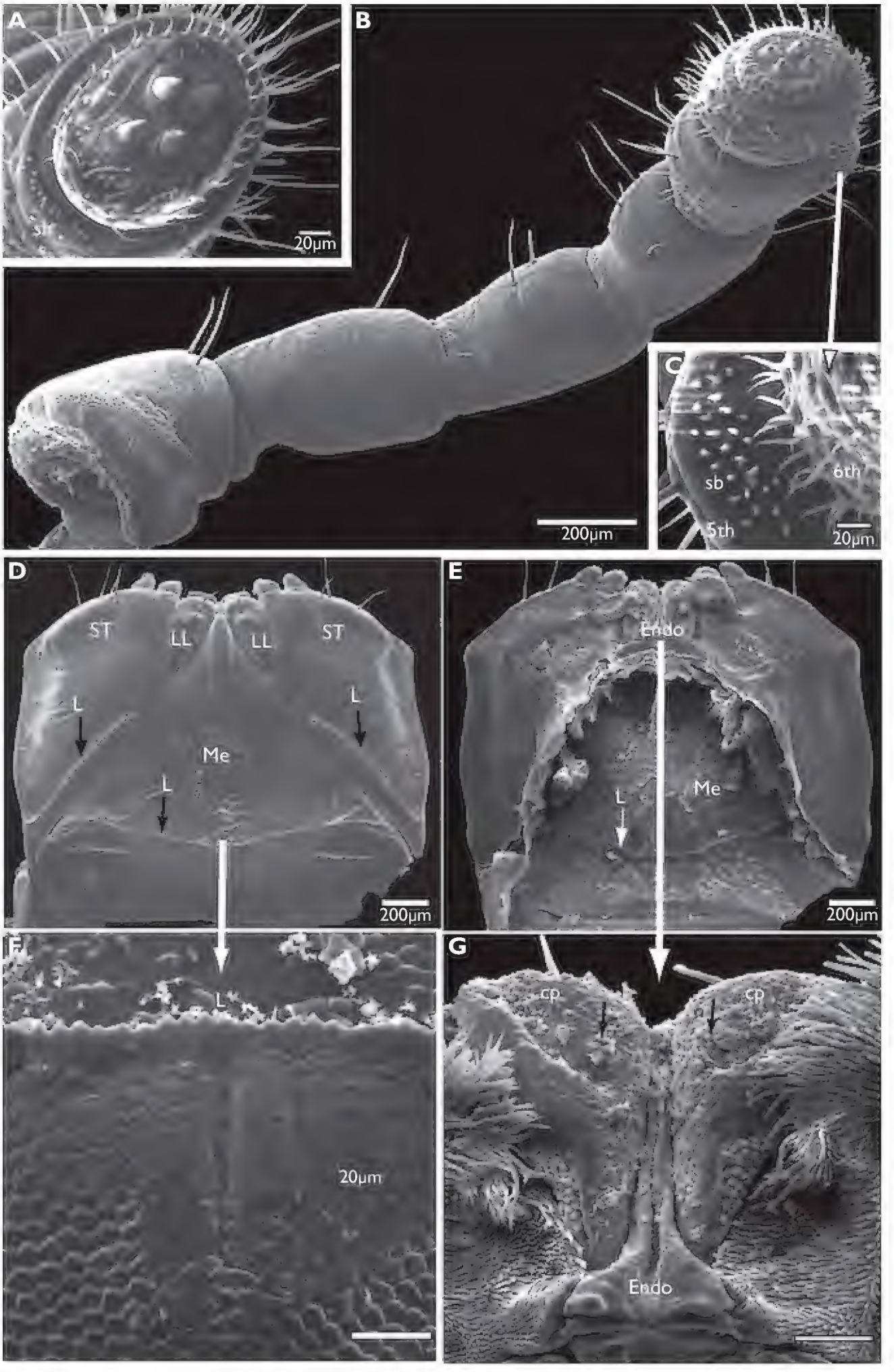

Figure 32. *Pseudocentrobolus aureus* sp. n. male paratype, SEM. **A** antenna, apical view **B** antenna, overview **C** antennomere 5 with sensilla basiconica; **D** gnathochilarium, ventral view **E** gnathochilarium, dorsal view **F** mentum of gnathochilarium, ventral view **G** endochilarium, dorsal view, arrow points to sensory cones. cp = endochilarium central pads; Endo = endochilarium; L = ledge; LL = lamella lingualis; Me = mentum; sb = sensilla basiconica; ST = stipites.

Gnathochilarium unusual (Fig. 32D). Lamellae linguales each with two standard setae located behind one another. Stipites each with three apical setae (Fig. 32D). Mentum basally subdivided by a well-developed suture (Figs 32D, F). Stipites each towards mentum with a wide sclerotized ledge (Fig. 32D). Palpi of gnathochilarium with numerous sensilla. Hypopharyngeal crest with a field of spine-like structures (Fig. 32E). Central pads of endochilarium separated into two areas: a group of 8–10 sensilla located apically, and medial palps with numerous sensilla each, located closely towards hypopharyngeal crest (Fig. 32G).

Mandible: external tooth simple, rounded; mesal tooth with three cusps (Fig. 33A). Six pectinate lamellae. Mesal margin of pectinate area (intermediate area) with circa four rows of small, slender spines. Molar plate with numerous (10 or 11) transverse furrows (Fig. 33A).

Collum: smooth, laterally longer than body ring 2 (Figs 31D, 36A). Lobe enlarged, laterally covering antenna and part of head (Fig. 31D).

Body rings: moniliform, overlapping one another up to anterior half of mesozona. Metazona of swollen appearance, width greater than those of pro- or mesozona. Transverse impressions covering mesozona (Fig. 33B), metazona with irregular punctations (Fig. 33C). Posterior margin of rings slightly excavated into rectangular extensions (Fig. 33C). Ozopores starting at ring 6, touching suture between mesozona and metazona (Fig. 31C).

Telson: anal valves with well-developed lips and micropunctation but with neither grooves nor setae. Preanal process well-rounded or sharp, extending beyond anal valves (Fig. 31C). Subanal scale inconspicuous.

Legs: coxae 1 and 2 elongated and fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae (Fig. 31E). Length of midbody legs circa 0.6 times body diameter in both sexes (Fig. 31F). Each podomere with an apical, ventral seta. Coxae 3 and beyond of rectangular shape (Fig. 31F). Tarsus with a stout dorso-apical setae and a pair of stout ventro-apical ones in males, in females with three pair of setae, apical pair stout, others successively much smaller.

Male sexual characters: tarsi 3 and beyond with a tarsal pad not protruding past base of claw. Coxae 3–7 with species-specific modifications.

Anterior gonopods: median sternal projection triangular, with a wide rectangular tip (Figs 35A, 49C). Sternite protruding almost as high as coxite and telopodite (Fig. 35A). Coxite wide, smoothly rounded, laterally curving around telopodite, on posterior side visible laterally as a small, triangular sclerite (Fig. 35B). Coxite anteriorly almost entirely covering telopodite (Fig. 35A). Telopodite with a short, well-rounded process. Process curved laterally, not or only slightly projecting above telopodite margin (Fig. 35B). Mesal margin elevated, laterally with a sharp ridge (Fig. 35B).

Posterior gonopods in situ almost completely covered by anterior gonopod. Suture separating coxite and telopodite well-visible. Sternite sclerotized and well-visible (Figs 31H, 34D). Finger-shaped process of coxite (Fig. 34D) not curved apically, but coaxial

to coxite. Coxite mesally with a single groove, basally wide, protruding into a short stem towards telopodite. Telopodite as long and as wide as coxite (Fig. 31G). Telopodites arranged face-to-face with one another (Figs 31G, H). A rounded disc present on apical part of telopodite (Figs 31G, H), disc covered with numerous tiny sclerotized

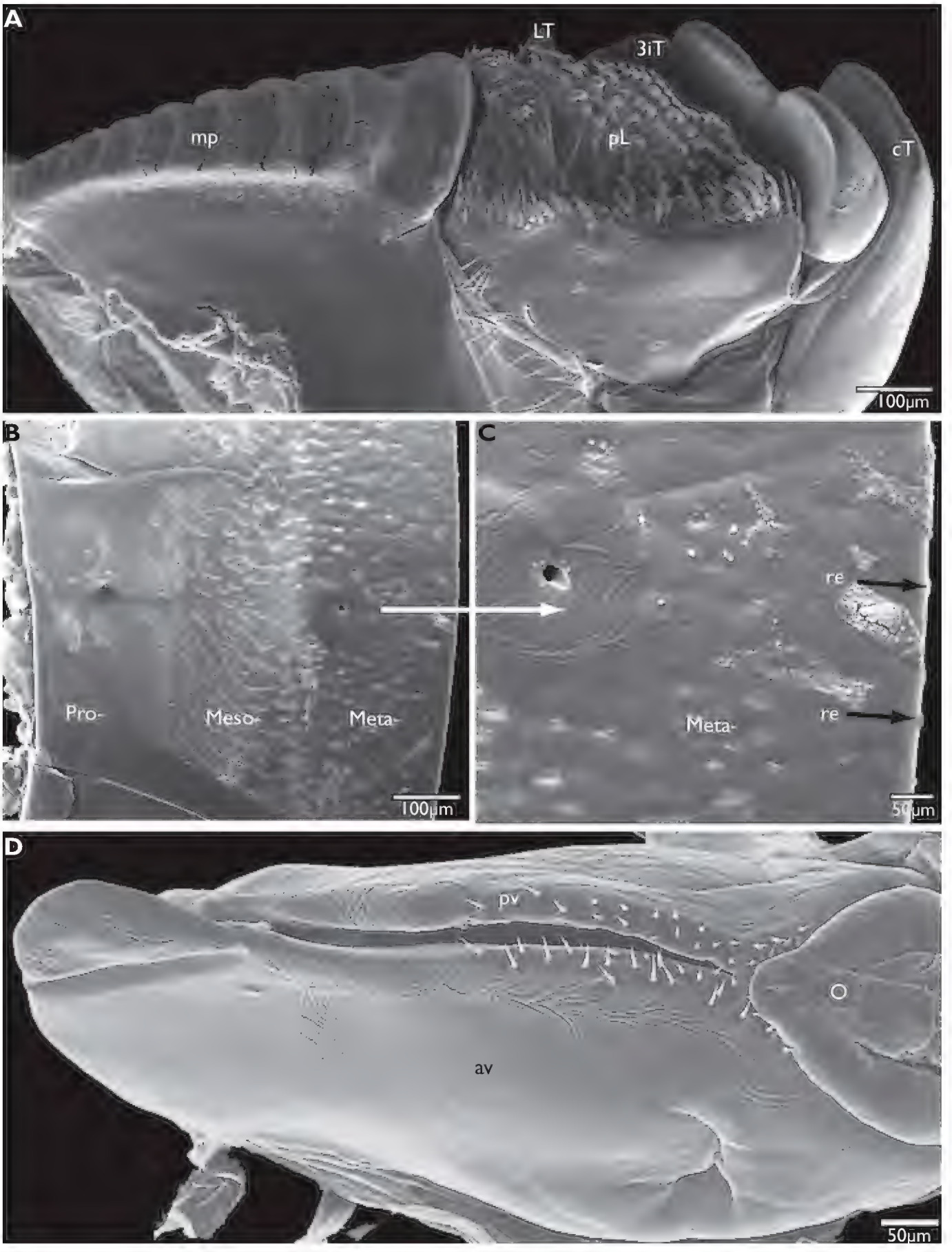

Figure 33. *Pseudocentrobolus aureus* sp. n. A–C male, D female paratype, SEM. **A** left mandible, mesal view **B** midbody ring, overview **C** midbody ring, detail of metazona **D** right vulva, lateral view. 3iT = 3-combed internal tooth; av = anterior valve; eT = external tooth; LT = lateral tooth; mp = molar plate; O = operculum; pL = pectinate lamella; pv = posterior valve; re = rectangular excavations.

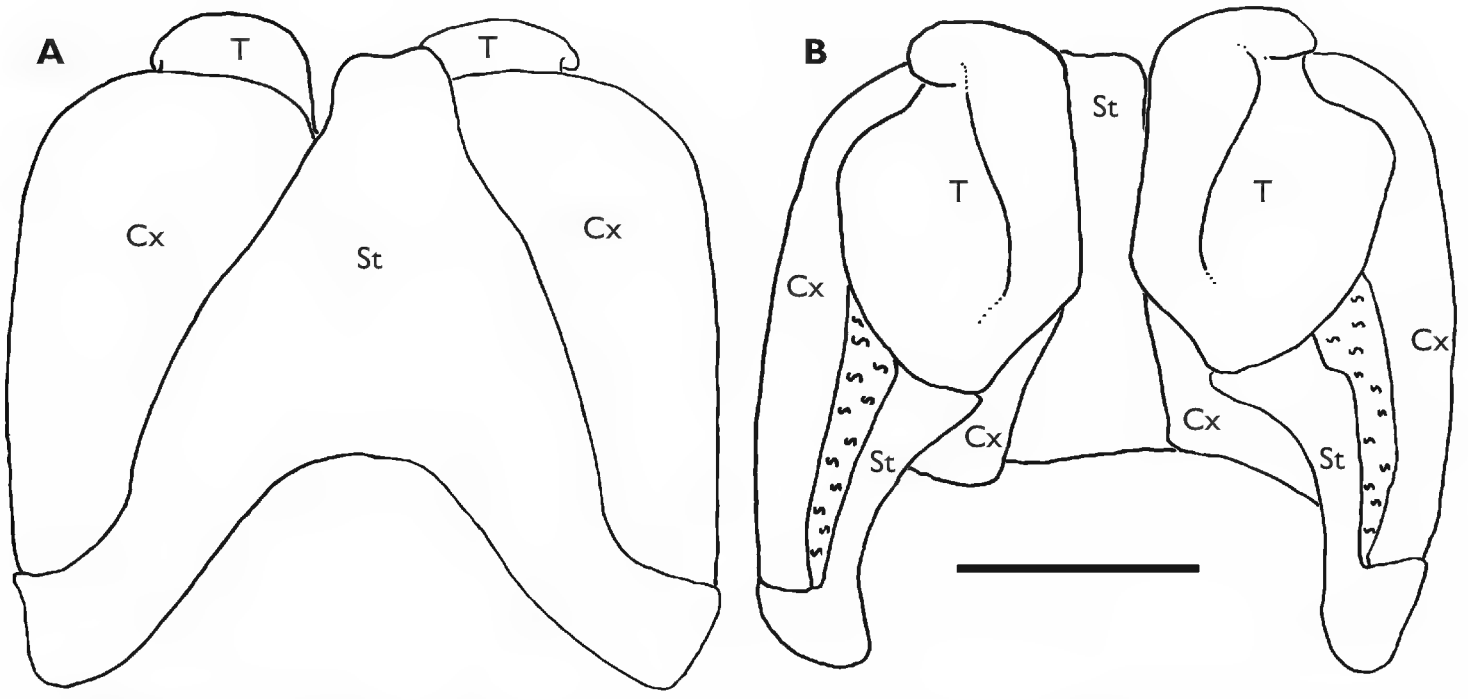

Figure 34. *Pseudocentrobolus aureus* sp. n., male holotype, anterior gonopod **A** anterior view **B** posterior view. Cx = coxite; St = sternite; T = telopodite. Scale bar = 1 mm.

teeth (Figs 34B, E), basally with a membranous process, into which sperm canal is discharging (Figs 34A, D, E).

Female sexual characters: vulva simple, bivalve-like, with a small, poorly sclerotized operculum at base (Fig. 33D). Anterior valve apically overlapping posterior one, both valves smooth, lacking sensory cones. Towards opening on each valve basally with two or three rows of setae (Fig. 33D).

Etymology: *Pseudocentrobolus*, masculine, refers to the superficial resemblance of species of this genus to some species of the South African genus *Centrobolus*.

Key to the *Pseudocentrobolus* species:

1 Mesozonites of body rings golden, metazonites black (Fig. 31C). Telson entirely golden (Fig. 31C). Antennae very short, protruding back to body ring 2 (Fig. 31D). Telopodite of anterior gonopod visible in anterior view (Fig. 34A). Telopodite of posterior gonopod only with a membranous process and a disc (Figs 35A, D) ..... ***P. aureus* sp. n.**

– Mesozonites of body rings greenish, metazonites golden (Fig. 35B). Telson anteriorly greenish, posteriorly golden (Fig. 35B). Antennae short, protruding back to body ring 4 (Fig. 35A). Telopodite of anterior gonopod completely covered by coxite in anterior view (Fig. 36C). Telopodite of posterior gonopod with a membranous process, a disc and an additional unique, finger-shaped process (Figs 36D, E) ..... ***P. vohibasiensis* sp. n.**

***Pseudocentrobolus aureus* Wesener, sp. n.**
urn:lsid:zoobank.org:act:7054A53D-190A-4AC4-813D-FEE9FCBF8269

Material examined: 34 ♂, 12 ♀, 1 imm. *Holotype:* 1 ♂ (42 mm long, dissected), CAS BLF 6071, Madagascar, Province Toliara, Forêt Beroboka, 5.9 km 131°SE Ankidranoka, tropical dry forest, 80 m, 22°13'59" S, 043°21'59" E, leg. Fisher, Griswold et al., 12–16.III.2002. *Paratypes:* 2 ♂, 1 ♀, CAS BLF 6071, same data as holotype; 11 ♂, 3 ♀, FMMC 5495, Forêt des Mikea, 7.5 km NE Tsifota, spiny bush forest, 60 m, 22°48.0' S, 43°26.0' E, leg. S. Goodman, pitfall trap, 25–26.II.2003; 4 ♂, 3 ♀, FMMC 5497, Forêt des Mikea, 9.5 km W. Ankiloaka, partially disturbed dry forest on red sands, 80 m, 22°46.7' S, 43°31.4' E, leg. V. Soarimalala, pitfall trap, 16–17.II.2003; 3 ♂, 9 ♀, FMMC 5501, same data as previous, but leg. S. Goodman, 14–15.II.2003; 8 ♂, FMMC 5506, same data as previous, but leg. S. Goodman, 16–17.II.2003; 2 ♂, FMMC 5681, Forêt des Mikea, 19 km SW Tanandava, 70 m 21°52.0' S, 43°39.6' E, leg. V. Soarimalala, pitfall trap, 22–24.III.2003.

Other material examined: 4 ♂, CASENT 9032809, Lake Ranobe, spiny forest, 30 m, 23°2.941' S, 43°36.635' E, leg. Frontier Wilderness Project, 21–28.I.2003.

Differential diagnosis: see key for a separation between *P. aureus* and *P. vohibasiensis* sp. n. The colour pattern of *Pseudocentrobolus aureus* is unique for Malagasy millipedes and allows for an easy identification.

Description. *Measurements*: males with 40 body rings, 40–48 mm long, 4.4–4.6 mm wide. Females with 39 or 40 body rings, 40–47 mm long, 4.9–5.0 mm wide.

Coloration affected by alcohol. Head, legs, antennae, telson and mesozonites of body rings golden. Metazonites of body rings black (Figs 31A–D). *Antennae* very short, protruding back to body ring 2 (Fig. 31D). *Male coxal processes* short and conical, only present on coxae 3 and 4. Coxae 5–7 slightly swollen in appearance (Fig. 31B). *Preanal process* well-rounded, prominently extending beyond anal valves (Fig. 31C).

Anterior gonopod sternite elongated into a wide, mesally slightly notched lobe (Fig. 34A). Coxite shorter than sternite (Fig. 34A). Telopodite on anterior side visible, on posterior side apically with a well-rounded process (Fig. 34B). Telopodite process short and well-rounded, laterally curved, only slightly longer than coxite (Fig. 34B).

Posterior gonopods: telopodite disc covered with numerous teeth (Fig. 35B). Membranous process well-developed, basally wide, apically slightly tapering (Fig. 35A).

Intraspecific variation: although specimens from the type series were collected from three different localities, no intraspecific variation of gonopods, colour or size was observed. Females are always 0.5 mm wider than males.

Distribution and ecology: this species was recorded from spiny forests close to the West Coast (Fig. 30).

Etymology: *aureus*, adjective, refers to the characteristic golden colour pattern of the species (Fig. 31A).

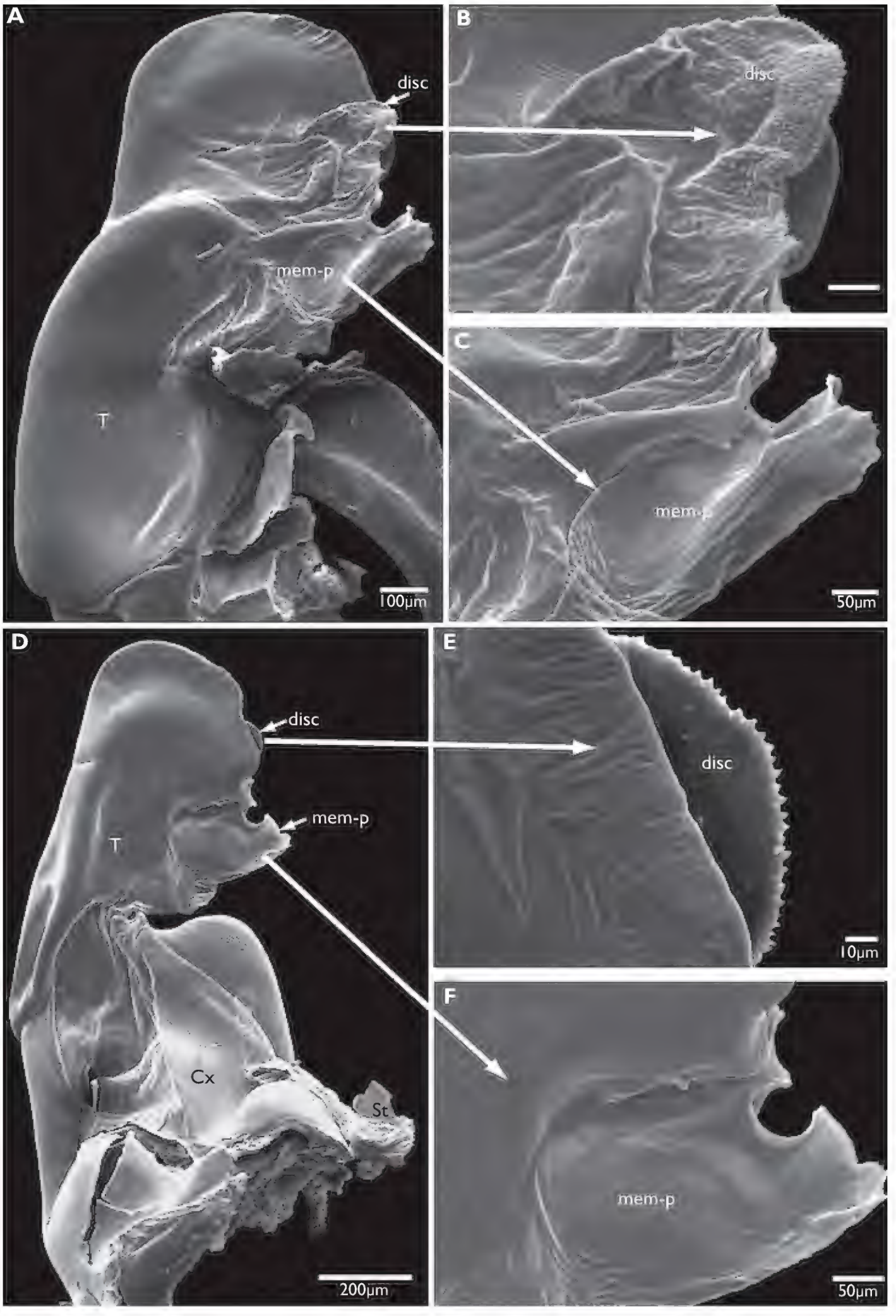

Figure 35. *Pseudocentrobolus aureus* sp. n., male paratype, A–C left, D–E right posterior gonopod. **A** overview, anterior view **B** detail of disc, anterior view **C** membranous process, anterior view **D** overview, posterior view **E** detail of disc, posterior view **F** detail of membranous process, posterior view. Cx = coxite; mem-p = membranous process; St = sternite; T = telopodite.

***Pseudocentrobolus vohibasiensis* Wesener, sp. n.**
urn:lsid:zoobank.org:act:5442A6D8-CF81-4A08-82D1-C3EEEFD037FE

Material examined: 3 ♂ *Holotype:* 1 ♂ (40 mm long), FMMC 8212, Madagascar, Province Toliara, Forêt de Vohibasia, subhumid forest, 780 m, 22°27.5' S, 44°50.5' E, leg. S. Goodman, 10–16.I.1996.

Other material examined: 1 ♂, CAS BLF 7390 (CASENT 9005836), Province Toliara, Forêt Analalava, Ranohira, dry forest on sand, 22°35'30" S, 45°7'42" E, leg. Fisher, Griswold et al. 1–5.II.2003; 2 ♂ (imm.), CAS BLF 7381, same data as previous, but pitfall trap; 1 ♂, CASENT 9032812, same data as previous, but beating low vegetation.

Differential diagnosis: *P. vohibasiensis* differs from *P. aureus* in the colour pattern and the presence of an additional sclerotized process on the posterior gonopods basally to the membranous process (Fig. 36D).

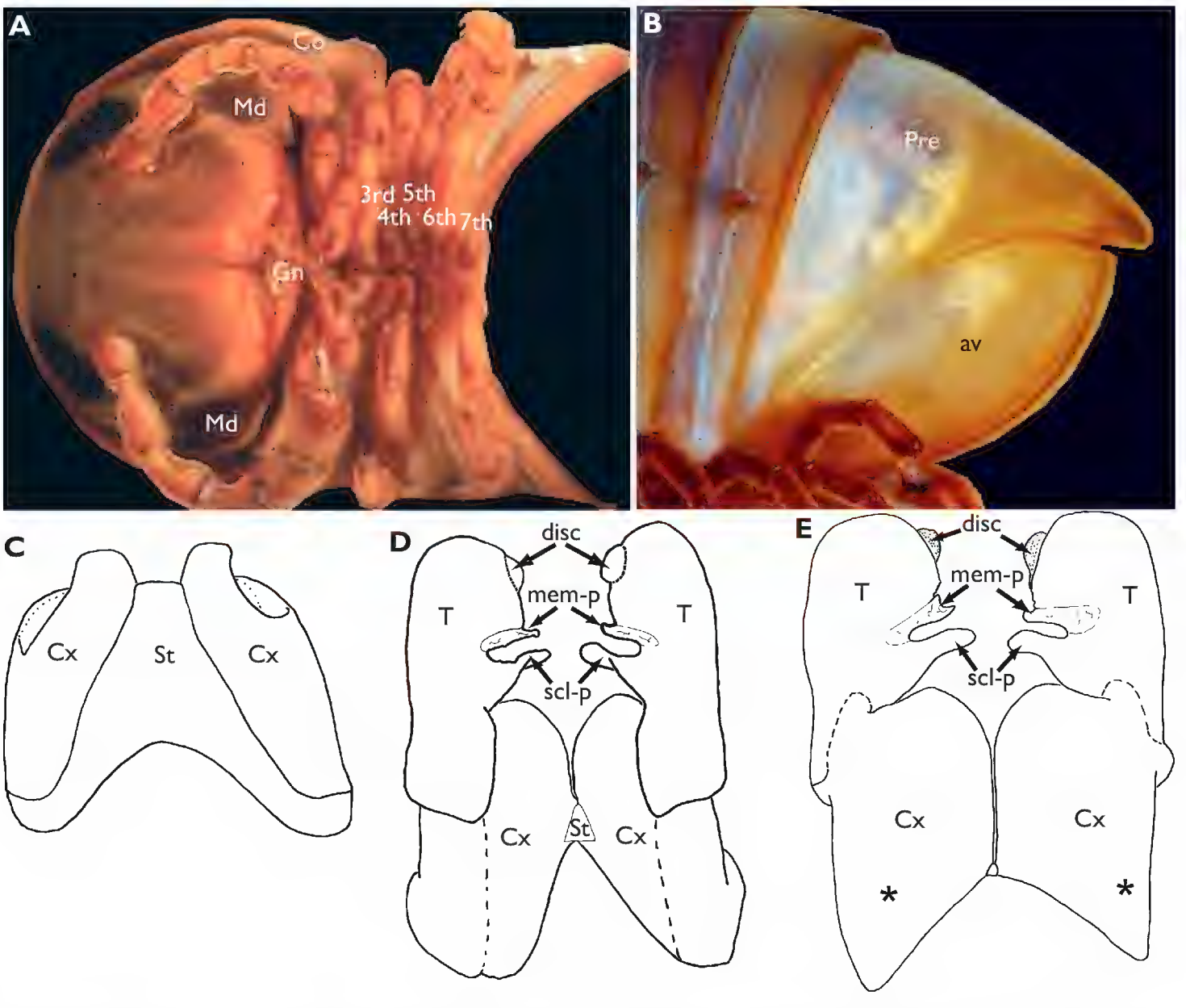

Figure 36. *Pseudocentrobolus vohibasiensis* sp. n., male holotype. **A** head and legs 1–7, ventral view **B** telson **C** anterior gonopod, anterior view **D** posterior gonopods, posterior view **E** posterior gonopods, anterior view. av = anal valves; Co = collum; Cx = coxite; Gn = gnathochilarium; Md = mandible; mem-p = membranous process; Pre = preanal ring; scl-p = sclerotized process; St = sternite; T = telopodite. Not to same scale.

Description. *Measurements*: male holotype with 38 body rings, circa 40 mm long, 4.3 mm wide.

Coloration faded in alcohol. Antennae and legs reddish (Fig. 36A). Head, collum, mesozona of body rings and anterior part of telson greyish-green (Fig. 36B). Metazona of body rings gold-brown (Fig. 36B).

Antennae protruding back to body ring 4 (Fig. 36A). *Male coxal processes* absent, but coxae 3–7 swollen (Fig. 36A). *Preanal process* well-rounded, longer than anal valves (Fig. 36B).

Anterior gonopod sternite elongated into a wide, broadly-rounded lobe (Fig. 36C). Coxite well-developed, in anterior view completely covering telopodite (Fig. 36C). Telopodite process short and well-rounded, laterally curved, not extending beyond telopodite (Fig. 36C).

Posterior gonopod telopodite disc covered with numerous teeth (Fig. 36E). Membranous process large, basally wide, apically slightly tapering (Figs 36D, E). Basally of membranous process with an additional long, finger-shaped process (Fig. 36E).

Distribution and ecology: known from the subhumid forest of Vohibasia and Analava (Fig. 30).

Etymology: *vohibasiensis*, adjective, after the type locality, Vohibasia.

Granitobolus Wesener, gen. n.

urn:lsid:zoobank.org:act:81CDE7E7-992A-42FD-9FCB-16D88FA8E7B9

Type species: *Granitobolus endemicus* sp. n.

Other species included:
G. andohahelensis sp. n.

Diagnosis: telopodite tip of posterior gonopods in *Granitobolus* uniquely shaped, resembling a duck's head with an acutely projecting beak (Fig. 37M). Adults with 37 or 38 body rings, lowest number of any Malagasy genus of Spirobolida. Natural colour usually contrasting, with red appendages, dark mesozonites and greyish or light brown metazonites (Figs 37A–D, 38A). Shares numerous characters only with species of the genus *Pseudocentrobolus*: a stout preanal process which extends beyond anal valves (Fig. 37F), well-developed lips on the anal valves, thick moniliform body rings which widely overlap each other reaching the metazonite (Fig. 37C), rectangular extensions (Fig. 37F) on the posterior margins of the rings and a greatly enlarged collum, which is ventrally longer than body ring 2. Gnathochilarium with a subdivided mentum and a single sclerotized ledge on each stipites (Fig. 37H), like in *Flagellobolus*, *Riotintobolus*, *Pseudocentrobolus*, *Caprobolus* **gen. n.**, *Alluviobolus* **gen. n.**, *Ostinobolus* **gen. n**. Both genera possess, however, completely different posterior gonopods.

Distribution and ecology: species of *Granitobolus* have been recorded from numerous rainforest and littoral rainforest sites in Southeast Madagascar. Unfortunately,

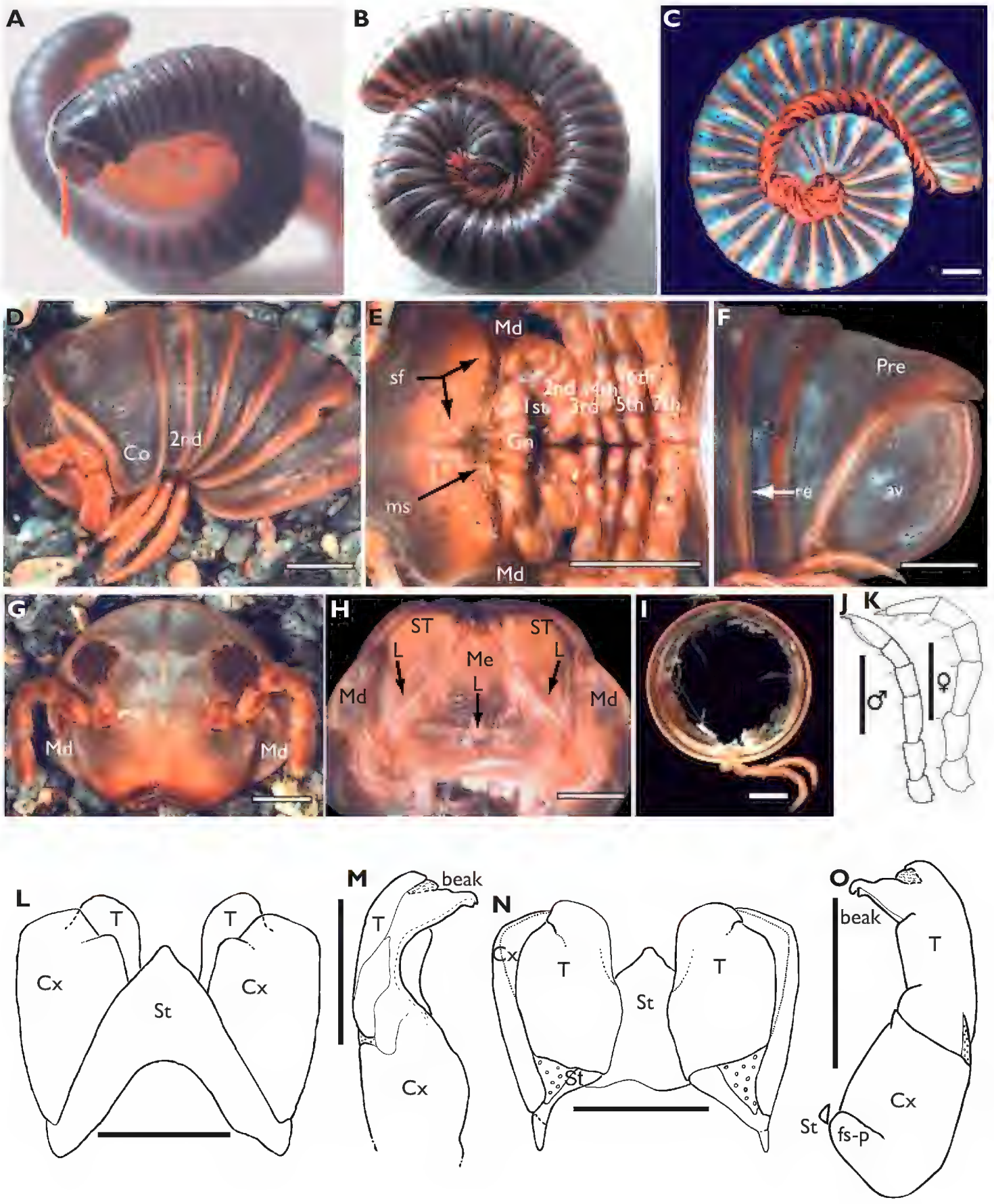

Figure 37. *Granitobolus endemicus* sp. n., A–C, G–J male paratype, K female paratype, D–F, L–O male holotype. **A** living specimen, uncurling **B** living specimen, curled **C** dead male, curled **D** head, lateral view **E** legs 1–7, ventral view **F** telson **G** head, frontal view **H** gnathochilarium, ventral view; **I** midbody ring with legs **J, K** left midbody legs **L** anterior gonopod, anterior view **M** left posterior gonopod, anterior view **N** anterior gonopod, posterior view **O** left posterior gonopod, posterior view. av = anal valves; Co = collum; Cx = coxite; fs-p = finger-shaped process; Gn = gnathochilarium; L = ledge; Md = mandible; Me = mentum; ms = marginal setae; Pre = preanal ring; re = rectangular extension; sf = setiferous foveolae; St = sternite; ST = stipites; T = telopodite. Scale bars = 1 mm.

mature males could be collected only from three sites (Andohahela-Vasiha, Manantantely and the Ambatotsirongorongo Mountain, Fig. 30). At least single immature specimens found in the littoral forest of Mandena and the Sainte Luce fragments S8 and S9 might represent another undescribed species because of their uniformly dark, almost black coloration. The specimens from Isaka-Ivondro (Andohahela), Ebosika (Andohahela) and Ivorona (Anosyenne) closely resemble *G. andohahelensis* sp. n. Except for two or three isolated specimens, which were collected on trails, all other specimens of *Granitobolus* were taken from large, massive, partly overgrown granitic outcrops. Specimens were collected in large numbers from thin layers of roots covering the stones. On a single rock, specimens of all sizes and both sexes were found; however, mature males remained rare. This might be related to the beginning of the dry season (June), when the collections were conducted. Both holotypes were infested with rather long nematodes (P, Fig. 38B). The legs and body rings of *G. endemicus* sp. n. holotype are also covered with fungi.

Description. *Males*: length up to 35 mm (broken), diameter up to 3.3 mm. 37 or 38 podous rings. Females: length up to 48 mm, diameter up to 4.85 mm. 37 or 38 podous rings. Length-width ratio in both sexes 1:10. Apodous rings absent in all adult specimens.

Colour: mesozona dark olive green or blackish (Fig. 37A), metazona much lighter, brown to yellow (Fig. 37C). Head, antennae and legs red (faded to light brown in some specimens).

Head: each eye large, with circa 35–40 ocelli arranged in 6 or 7 vertical rows (Figs 37D, G). Labrum with standard three irregular teeth and one row of 10–12 stout marginal setae (Fig. 37E). Clypeus with two setiferous foveolae on each side (Fig. 38B). Length of antennae sexually dimorph, protruding back to ring 2 (females) or 4 (males, Figs 37A, D, 38A). Relative lengths of antennomeres: 1<2=3=4=5<6 (Fig. 37G). Terminal antennomere with four large sensory cones located together inside a membranous area. Antennomere 5 latero-apically with three or four rows, antennomere 6 with two rows of sensilla basiconica.

Gnathochilarium unusual (Fig. 37H). Lamellae linguales each with two standard setae located behind one another. Stipites each with three apical setae. Mentum basally subdivided by a well-visible suture (Fig. 37H). Stipites each towards mentum with a wide sclerotized ledge (Fig. 37H). Hypopharyngeal crest with a field of spine-like structures. Central pads of endochilarium separated by a step into two levels. Medial palps with a large group of sensilla each, located towards hypopharyngeal crest.

Mandible: external tooth simple, rounded; mesal tooth with three cusps. Four pectinate lamellae. Molar plate with numerous (10 or 11) small and shallow transverse furrows.

Collum: smooth, laterally longer than body ring 2. Lobe enlarged, covering antenna and part of head (Figs 37D, 38A).

Body rings: moniliform, overlapping up to anterior half of mesozona. Metazona of swollen appearance, width larger than pro- or mesozona (Figs 37A–C). Posterior margin of rings slightly excavated into rectangular extensions (Fig. 37F). Ozopores starting at ring 6, touching suture between mesozona and metazona (Fig. 37D).

Telson: anal valves with well-developed lips and micropunctation, but with neither grooves, nor setae. Preanal process well-rounded or sharp, extending beyond anal valves (Figs 37F, 38C). Subanal scale inconspicuous.

Legs: coxae 1 and 2 elongated, fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae. Length of midbody legs circa 1.0 times body diameter in males (Fig. 37J), 0.6 times body diameter in females (Fig. 37K). Each podomere with an apical, ventral seta (Fig. 37K). Coxae 3 and beyond of rectangular shape (Fig. 37I). Tarsus with a stout dorso-apical seta and a pair of stout ventro-apical ones in males, three pairs of setae in females. In females apical setae pair stout, others successively much smaller.

Male sexual characters: tarsi starting at leg 3 up to midbody legs wide and with a large tarsal pad not protruding past base of claw (Fig. 37J). Tibia shorter than in females (Figs 37J, K). Coxae 3–7 unmodified (Figs 37E, 38B).

Anterior gonopods: median sternal projection triangular, with a wide, rectangular tip (Figs 37L, 38D). Sternite never protruding as high as coxite. Coxite wide, smoothly rounded, laterally curving around telopodite, but only extending slightly at posterior side (Figs 37N, 38F). Coxite anteriorly almost completely covering telopodite. Coxite

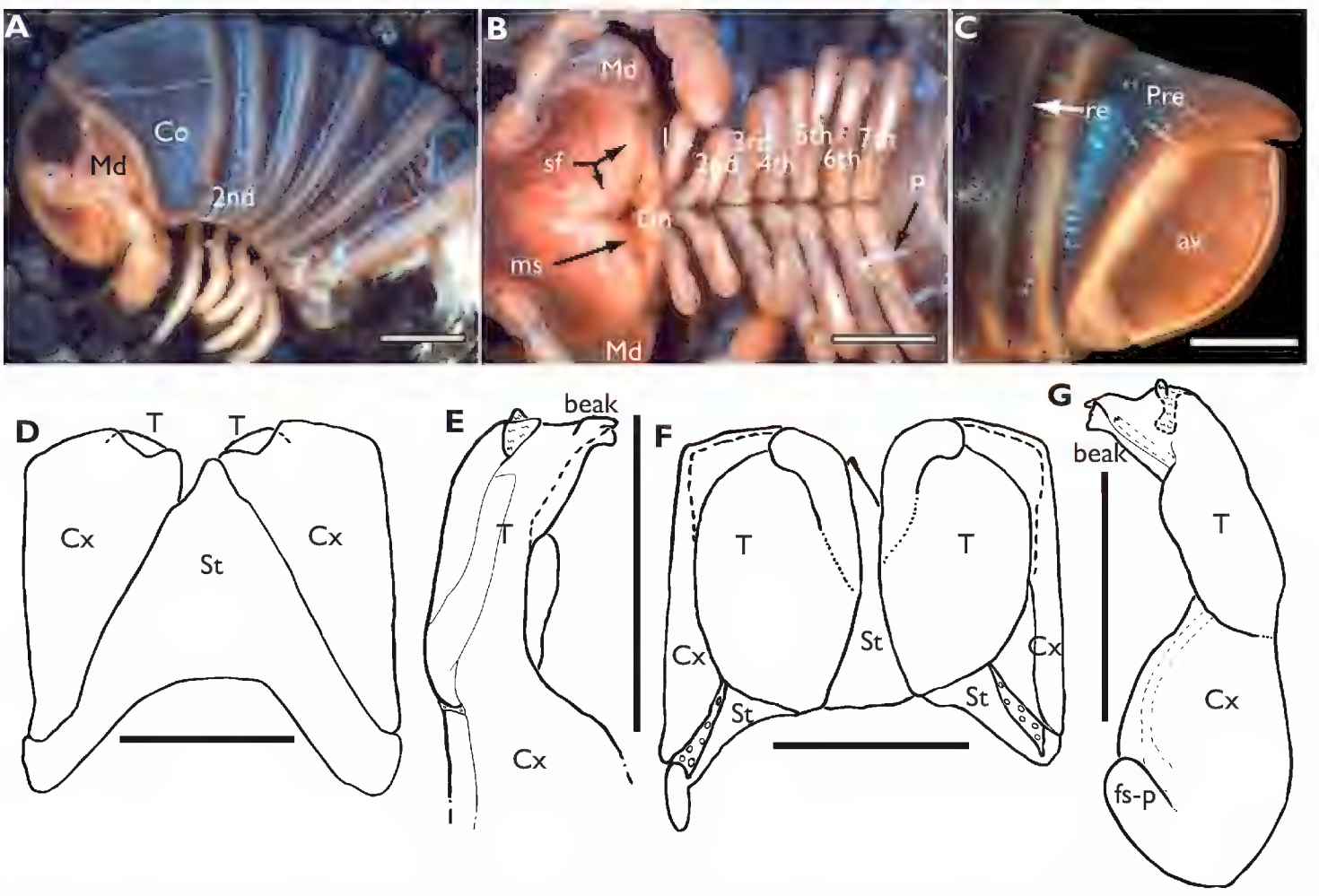

Figure 38. *Granitobolus andohahelensis* sp. n., male holotype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** anterior gonopod, anterior view; **E** left posterior gonopod, anterior view **F** anterior gonopod, posterior view **G** left posterior gonopod, posterior view. av = anal valves; Co = collum; Cx = coxite; fs-p = finger-shaped process; Gn = gnathochilarium; Md = mandible; ms = marginal setae; P = parasitic nematode?; Pre = preanal ring; re = rectangular extension; sf = setiferous foveolae; St = sternite; T = telopodite. Scale bars = 1 mm.

processes absent, but mesal margin towards sternite sometimes projecting (Fig. 37L). Telopodite with a short, well-rounded, laterally curved process, which only slightly projects above telopodite margin and never protrudes above coxite margin (Figs 37N, 38F).

Posterior gonopods in situ almost completely covered by anterior gonopods. Suture between coxite and telopodite well-visible (Fig. 37O), sternite triangular and sclerotized but often hidden by a large, finger-shaped coxite process (Fig. 37O). Finger-shaped process not curved, running parallel to basal margin (Figs 37O, 38G). Telopodites arranged face-to-face with one another (Fig. 37M). Shape of apical part resembling 'beak' (Figs 37M, 38E). Beak acutely projecting, partly sclerotized and carrying sperm canal (Fig. 38G). Telopodite between apex and beak with a small membranous area (Fig. 37M), in basal half mesally of sperm canal with a lower elevated area (Fig. 37M).

Female sexual characters: vulva simple, with a small, poorly sclerotized operculum at base, bivalve-like. Posterior valve apically slightly overlapping anterior one. Both valves smooth, sensory cones absent. Each valve basally towards opening with two rows of setae.

Etymology: *Granitobolus*, masculine, after Granit (German for granite) for the special habitat, granitic outcrops, on which species of this genus were found, and *-bolus*.

Key to the *Granitobolus* species:

1 Telopodite of anterior gonopod with a weakly-developed process, not reaching mesal margin (Fig. 37N). Mesal margin of coxite at midpoint projecting towards sternite (Fig. 37L). Apex of posterior gonopod telopodite covered with a sclerite (Fig. 37M) ..... ***G. endemicus* sp. n.**

– Telopodite process of anterior gonopod prominent, starting at mesal margin (Fig. 38F). Mesal margin of coxite not projecting (Fig. 38D). Apex of posterior gonopod telopodite covered with a membranous area (Fig. 38E) ..... ***G. andohahelensis* sp. n.**

***Granitobolus endemicus* Wesener, sp. n.**
urn:lsid:zoobank.org:act:7EFB7119-B5B1-4D30-BE97-F9F709EDD92B

Material examined: 1 ♂, 6 ♀, 14 imm. *Holotype:* 1 ♂ (35 mm long), FMMC W010A, Madagascar, Province Toliara, Ambatotsirongorongo Mountain, Forêt Petit Lavasoa, rainforest, 25°05.021' S, 46°46.110' E, leg. Wesener et al., 21.V.2007. *Paratypes:* 3 ♀, 6 imm., FMMC W010A, same data as holotype; 1 ♀, ZMH W010A, same data as holotype.

Other material examined: 2 ♀, 7 imm., W010A, same data as type material, but stored as vouchers at University Antananarivo; 1 imm., FMMC W099, Ambatotsirongorongo Mountain, Forêt Grand Lavasoa, 25°5'10.23" S, 46°44'55.93" E, rainforest, leg. Wesener et Schütte, 14.VI.2007.

Differential diagnosis: see key for a separation between *G. endemicus* and *G. andohahelensis* sp. n.

Description. *Measurements*: male with 37 rings, circa 35 mm long (broken), 3.5 mm wide. Females with 37 or 38 rings, 42–48 mm long, 3.8–4.9 mm wide.

Coloration affected by alcohol. Anterior part of head and appendages red (Figs 37D, G). Mesozona and anterior part of metazona dark grey, posterior part of metazona light brown to dark orange (Figs 37A–C). *Antennae* very short, in males protruding back to body ring 3 (Fig. 37D), in females to ring 2. *Preanal process* well-rounded, longer than anal valves (Fig. 37F).

Anterior gonopod sternite elongated into a short, wide and well-rounded lobe (Fig. 37L). Mesal margin of coxite at midpoint with a projection towards sternite (Fig. 37N). Telopodite on posterior side apically with a short, rounded process (Fig. 37N). Telopodite process not reaching mesal margin, laterally curved, slightly longer than coxite (Fig. 37N).

Posterior gonopods: telopodite apex erect, covered by a sclerite (Fig. 37M). A small membranous area present between apex and beak (Fig. 37O).

Intraspecific variation: too few specimens, especially mature males, are known to evaluate the intraspecific variation. However, obviously mature females collected at the same spot range from 35 to 48 mm of length, most likely representing different stadia, or even generations.

Distribution and ecology: this species is currently known only from, and probably microendemic to, the isolated rainforests of the Ambatotsirongorongo Mountain in Southeast Madagascar (Fig. 30), covering altogether less than 10 km^2. The Mountain is now isolated from all other natural forests. The forest cover of the Ambatotsirongorongo Mountains decreased considerably in the last 50 years (Ramanamanjato et al. 2002) and covers now only a few hundred hectares (Moat and Smith 2007). The nearest remaining forest is the worldwide unique, and also endangered, transitional littoral forest of Petriky, 5 kilometers north of Ambatotsirongorongo.

Etymology: *endemicus*, adjective, refers to the small area of distribution (Fig. 30).

***Granitobolus andohahelensis* Wesener, sp. n.**
urn:lsid:zoobank.org:act:D022AF86-E072-4090-B604-F7D5A3C8F425

Material examined: 4 ♂, 7 ♀, 32 imm. *Holotype:* 1 ♂ (33 mm long), FMMC 13603, Madagascar, Province Toliara, Andohahela, Mt. Vasiha, 500 m, 24°55'19" S, 46°44'45" E, station 12, on 15° slope, E of summit, no granite outcrops, leg. K. Emberton, 6.II.1995. *Paratypes:* 1 ♂, 1 ♀, 8 imm., FMMC W045, Parc National de Andohahela, Malio, rainforest, 24°55.810' S, 46°46.343' E, leg. Wesener et al., 30.V.2007; 1 ♂, 1 ♀, ZMUC W045, same data as previous; 1 ♀, 2 imm., ZMH W045, same data as previous.

Other material examined: 1 ♀, 12 imm., W045, same data as previous material, but stored as vouchers at University Antananarivo; 1 ♂, 1 ♀, 4 imm., FMMC W078, Province Toliara, Manantantely, 24°59'17.14" S, 46°55'27.95" E, rainforest, leg. Wesener et Schütte, 06.VI.2007; 1 ♀, ZMH W078, same data as previous; 1 ♀, 6 imm., W078, same data as previous, University Antananarivo.

Differential diagnosis: *G. andohahelensis* differs from *G. endemicus* in a slightly different colour pattern and differently shaped telopodites of the anterior (Fig. 38F) and posterior gonopods (Fig. 38G).

Description. *Measurements*: males with 37 or 38 rings, circa 31–35 mm long (broken), 3.3–3.5 mm wide. Females with 38 rings, 37–43 mm long, 3.7–4.1 mm wide.

Coloration affected by alcohol. Anterior part of head and appendages white to reddish (Fig. 38A). Mesozona and anterior part of metazona dark grey, posterior part of metazona dark orange (Figs 38A–C). *Antennae* very short, in males protruding back to ring 4 (Fig. 38A), in females to ring 2. *Preanal process* well-rounded, extending beyond anal valves (Fig. 38C).

Anterior gonopod sternite elongated into a short, well-rounded lobe (Fig. 38D). Coxite large, inconspicuous, with neither processes, nor projections (Fig. 38D). Telopodite visible on anterior side, on posterior side apically with a rounded process (Fig. 38F). Telopodite process starting at mesal margin, laterally curved, slightly extending beyond coxite (Fig. 38F).

Posterior gonopods: telopodite apex not erect, covered by a membranous area (Fig. 38G). A membranous area present between apex and beak, with a short process projecting above margin (Fig. 38E).

Intraspecific variation: the specimens from Manantantely display, in comparison with the holotype from Vasiha, small differences on the beak of the posterior gonopod. These differences are now regarded as intraspecific variation. No variation at all was observed between the holotype collected in Vasiha 1995 and those collected few hundred meters East in Malio 2007 (Fig. 30). Like in *G. endemicus*, females of different size classes are present.

Distribution and ecology: known from the rainforest of Malio, as well as 20 km east from the forest of Manantantely (Fig. 30). It is currently unclear if similar specimens collected from Ebosika, the Isaka-Ivondro corridor and Ivorona also belong to *G. andohahelensis*, Single specimens taken from the littoral forests of Mandena and Sainte Luce show a uniformly black coloration and most likely belong to a yet undescribed species. All specimens of *G. andohahelensis* were collected in thin root layers covering large granitic outcrops.

Etymology: *andohahelensis*, adjective, after the type locality.

Caprobolus Wesener, gen. n.

urn:lsid:zoobank.org:act:23C9C435-1012-44AE-8FF1-82C471F2A0E4

Type species: *Caprobolus andringitra* sp. n., monotypic

Diagnosis: mandible with a very short molar plate (Fig. 40F), so far a unique character (but the shape of the mandible is only known for a few genera of Spirobolida). Anterior and posterior gonopods of *Caprobolus* are unique for Spirobolida. Anterior gonopods with a conspicuously enlarged, slender sternite (Fig. 41A), but sternite still

much wider than in *Spiromimus* (Wesener and Enghof, 2009). Telopodite of anterior gonopods prominently enlarged into unique, long, slender, sabre-like processes (Fig. 41B). Basis of telopodite process projecting into a slender, well-rounded retrorse process (Fig. 41B), which is present in numerous genera of Spirobolida. Telopodite of posterior gonopod longer than, but as wide as, coxite (Fig. 41C). Telopodite basally deeply divided into two branches of almost similar width and length (Figs 41C–E). Sperm canal is free, starting at basis of telopodite, only slightly attached to shorter, lateral main branch (Fig. 41E). Sperm canal projecting as a flagellum above telopodite branches (Fig. 41D). Shares a reddish colour pattern and a yellowish dorsal stripe with *Spiromimus* de Saussure & Zehntner, 1901, *Alluviobolus* gen. n. and *Ostinobolus* gen. n. Gnathochilarium with a subdivided mentum and a single sclerotized ledge on each stipites (Fig. 39E), like in *Flagellobolus*, *Riotintobolus*, *Pseudocentrobolus*, *Granitobolus*, *Alluviobolus* gen. n., *Ostinobolus* gen. n.

Distribution and ecology: only known from the rainforests of Andringitra, close by Ivohibe and Vevembe, located at the edge of the high plateau towards the east coast in the southern half of Madagascar (Fig. 30). The only known species of *Caprobolus* was collected in Andringitra together with a *Spiromimus* species.

Etymology: *Caprobolus*, masculine, composed of *Capro-*, formed after *capricornus*, which refers to the tropic of Capricorn where this genus was first collected, and *-bolus*.

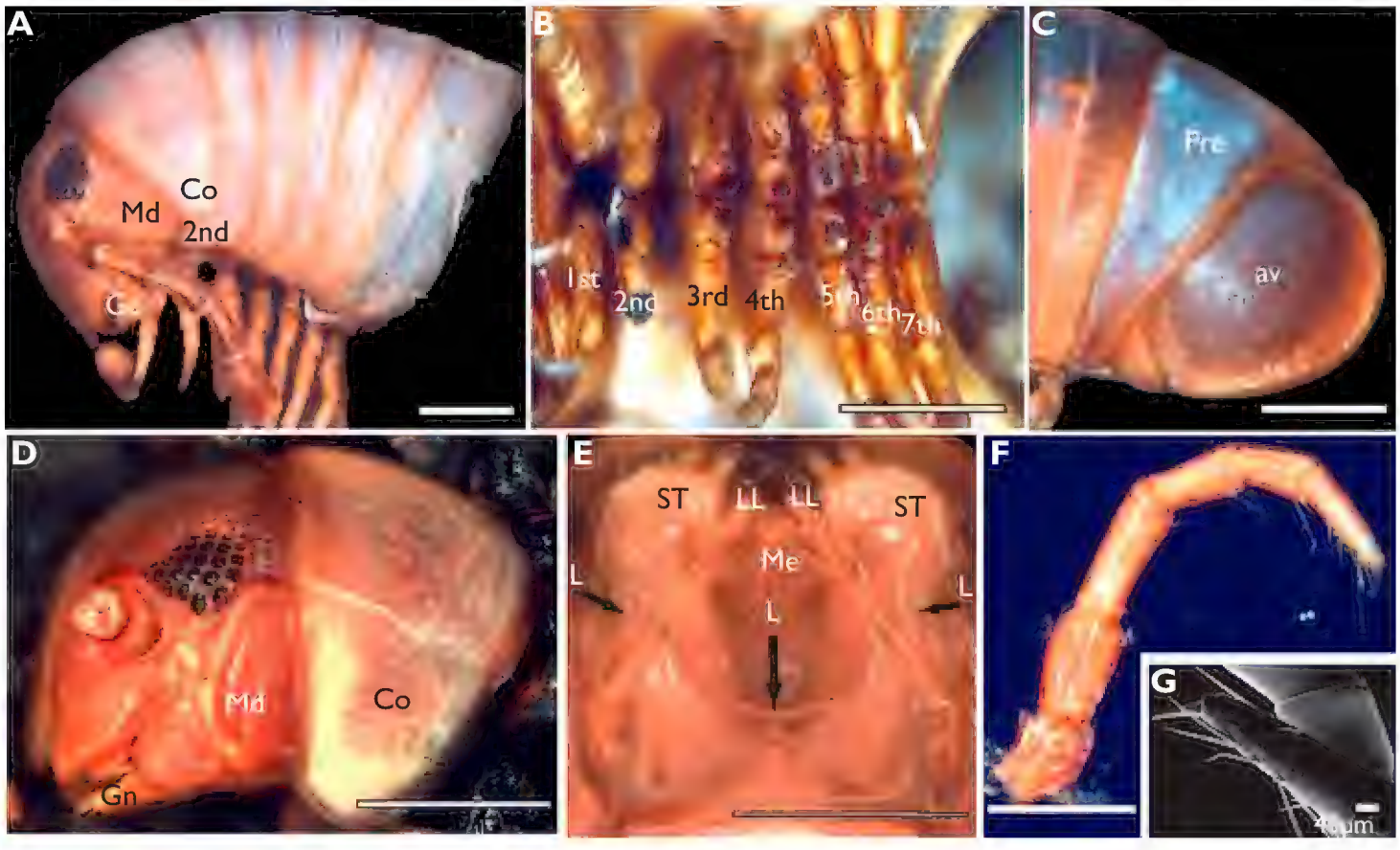

Figure 39. *Caprobolus andringitra* sp. n., A–C male holotype, D–G male paratype **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** head, detail of eye and mandible **E** gnathochilarium, ventral view **F** right midbody leg, overview **G** tarsus of midbody leg, SEM. av = anal valves; Co = collum; Gn = gnathochilarium; L = ledge; LL = lamella lingualis; Md = mandible; Me = mentum; Pre = preanal ring; re = rectangular extension; ST = stipites. Scale bars = 1 mm.

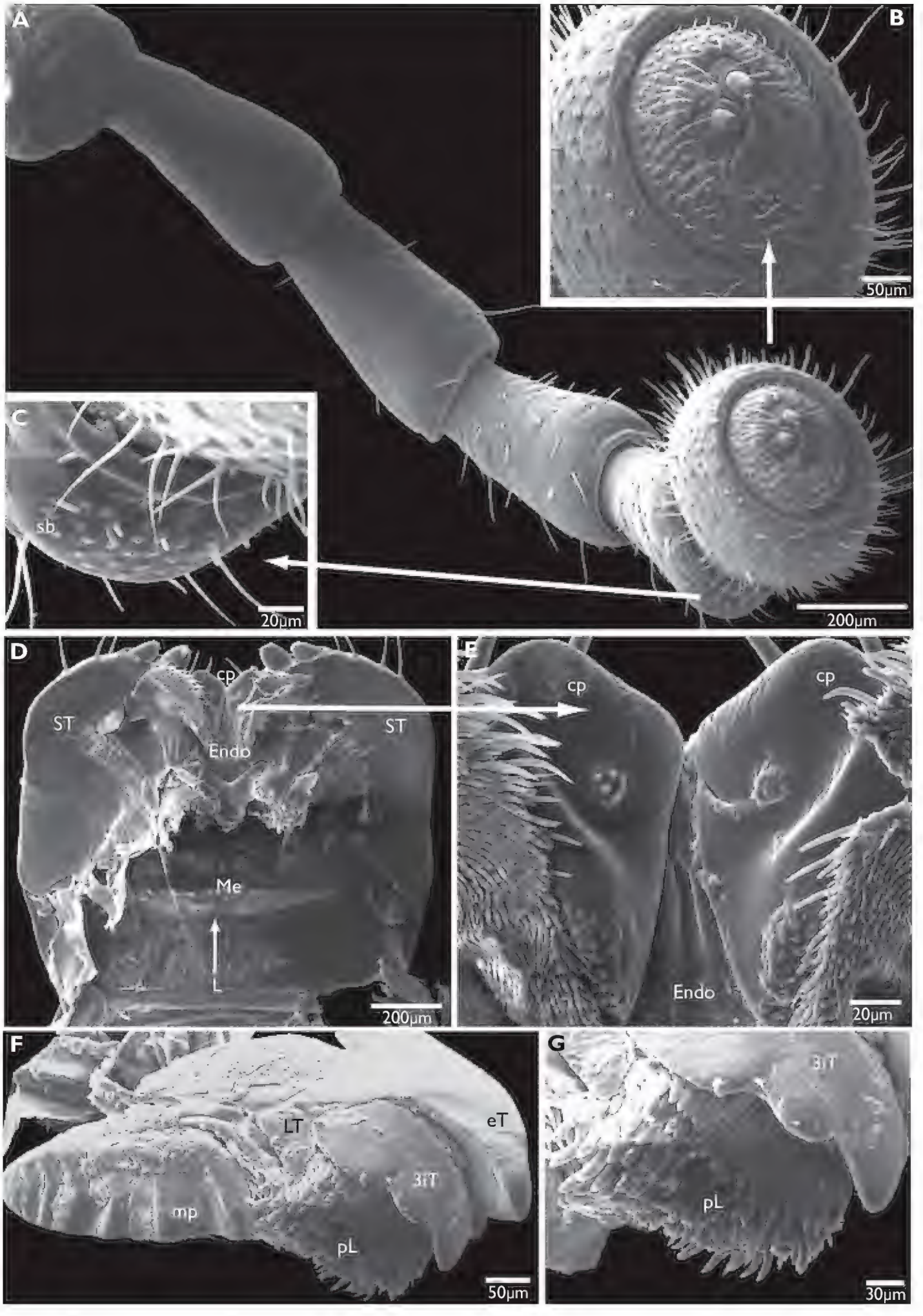

Figure 40. *Caprobolus andringitra* sp. n. male paratype, SEM. **A** antenna, overview **B** antenna, apical view on disc **C** antennomere 5 with sensilla basiconica **D** gnathochilarium, ventral view **E** endochilarium detail **F** left mandible, mesal view **G** mandible, detail of pectinate lamella. 3iT = 3-combed internal tooth; cp = central pads of endochilarium; Endo = endochilarium; eT = external tooth; L = ledge; LT = lateral tooth; Me = mentum; mp = molar plate; pL = pectinate lamella; sb = sensilla basiconica; ST = stipites.

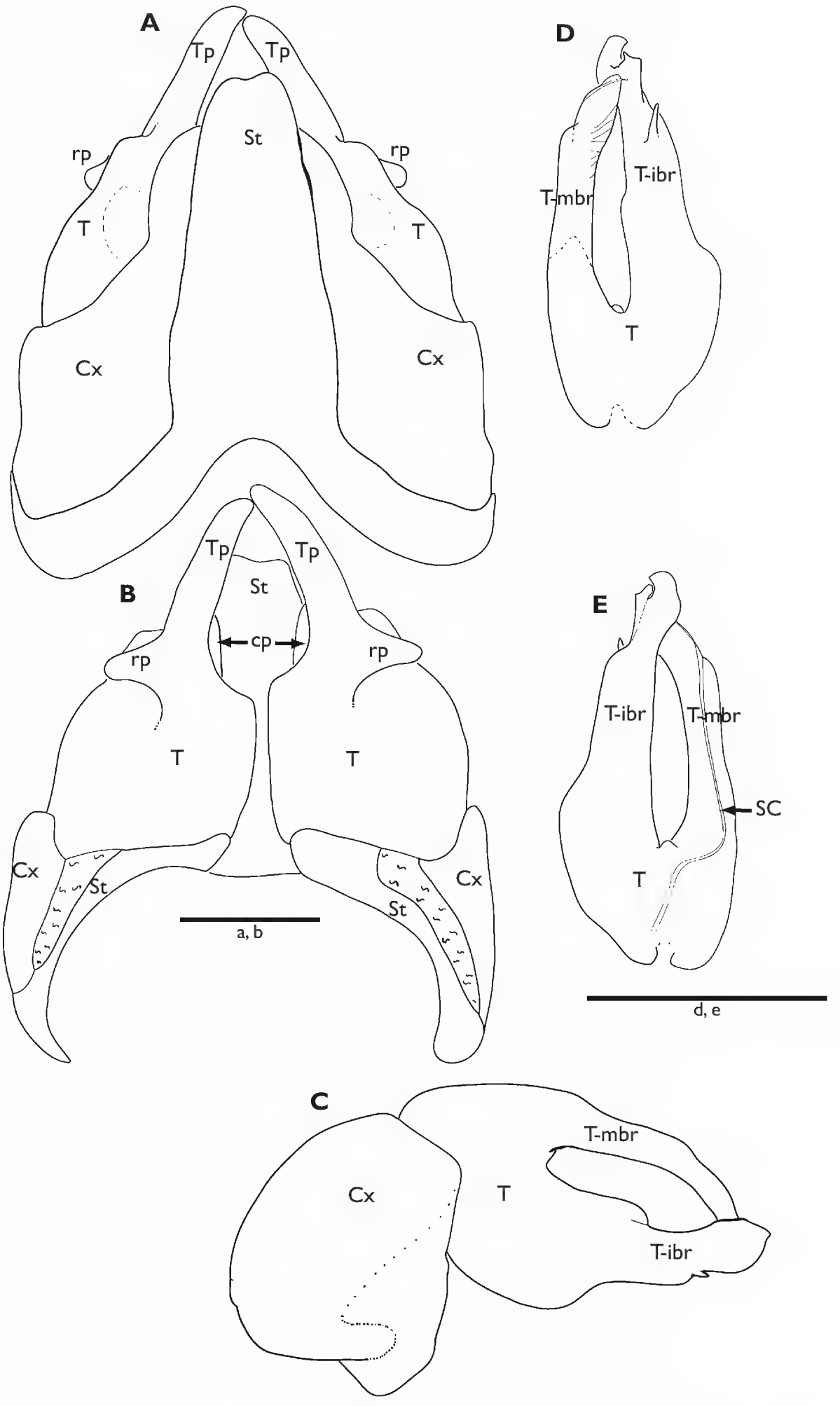

Figure 41. *Caprobolus andringitra* sp. n., male holotype. **A** anterior gonopod, anterior view **B** anterior gonopod, posterior view **C** right posterior gonopod, posterior view **D** right posterior gonopod, telopodite, posterior view **E** right posterior gonopod, telopodite, anterior view. cp = internal coxite process; Cx = coxite; rp = retrorse process; SC = free sperm canal; St = sternite; T = telopodite; T-ibr = inner branch of telopodite; T-mbr =main branch of telopodite; Tp = telopodite process. Scale bars = 1 mm.

***Caprobolus andringitra* Wesener, sp. n.**
urn:lsid:zoobank.org:act:331040CB-492C-483D-8D12-41B8265EB54D

Material examined: 6 ♂, 1 imm. *Holotype:* 1 ♂ (41 mm long), FMNH-INS 13601, Madagascar, Province Fianarantsoa, Andringitra reserve, camp 3, 40 km S Ambalavao, along Volotsangana River, rainforest, 1210 m, 22°13'22" S, 46°58'18" E, leg. S. Goodman, 5–6.XII.1993. *Paratypes:* 3 ♂, 1 imm., FMNH-INS 13600, same data as holotype; 1 ♂, FMNH-INS 13611, same data as holotype; 2 ♂, FMMC 8219, RS Ivohibe, 900 m, rainforest, 22°25' S, 46°56 'E, leg. S. Goodman, 7–12.X.1997.

Other material examined: 1 ♂, CASENT 9032814, Province Fianarantsoa, Forêt de Vevembe, 66.6 km 293°WNW Farafangana, rainforest in transition to montane rainforest, 600 m, 22°47'28" S, 47°10'55" E, leg. B. L. Fisher et al., yellow pan trap, 23.IV.2006

Description. *Measurements*: male holotype with 44 rings, circa 41 mm long, 3.2 mm wide. Male paratypes with 43 or 44 rings (specimen from Vevembe with 46), up to 44 mm long, up to 3.5 mm wide.

Coloration faded in alcohol. Head, legs and antennae orange-red (Figs 39A–D). Anal valves and subanal scale reddish, preanal process greyish (Fig. 39C). Metazonites red, remaining parts of body rings up to ozopore openings orange-reddish, more dorsally greyish. Specimens dorsally with a slender, orange line.

Head: each eye with circa 24–28 ocelli arranged in 6 or 7 vertical rows (Fig. 39D). Labrum with standard three irregular teeth and a single row of 10–12 stout marginal setae. Clypeus with two setiferous foveolae on each side. Antennae long, protruding back to ring 6. Relative lengths of antennomeres: 1<<2=3=4=5=6, first antennomere very short (Fig. 40A). Terminal antennomere with four large sensory cones located together inside a membranous area (Fig. 40B). Antennomere 5 latero-apically with five rows (Fig. 40C), antennomere 6 with two rows (Fig. 40B) of sensilla basiconica.

Gnathochilarium lamellae linguales each with two standard setae located behind one another (Fig. 39E). Stipites each with three apical setae. Palpi of gnathochilarium with numerous sensilla. Hypopharyngeal crest with a field of spine-like structures (Fig. 40D). Central pads of endochilarium separated into two areas, a group of 6–8 sensilla located apically (Fig. 40E). Close to endochilarium with a large group of sensilla, located towards hypopharyngeal crest. Mentum basally subdivided by a membranous suture (Fig. 39E). Stipites each with a sclerotized ledge (Fig. 39E)

Mandible external tooth simple, rounded; mesal tooth with three cusps (Fig. 40F). Seven to nine dense pectinate lamellae (Fig. 40G). Intermediate area between pectinate lamellae and molar plate almost completely absent. Molar plate short, only slightly longer than pectinate lamellae, with only six or seven transverse furrows (Fig. 40F).

Collum: smooth, not protruding as far as body ring 2 (Fig. 39A).

Body rings: mostly smooth, with some irregular punctation and some transverse impressions on mesozona. Ozopores starting at ring 6, touching suture between mesozona and metazona. Ozopore on ring 6 located more ventrally than subsequent ozopores.

Telson: anal valves with well-developed lips and micropunctation. Preanal ring and subanal process well-rounded, not extending beyond anal valves (Fig. 39C).

Legs: coxae 1 and 2 elongated and fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae. Length of midbody legs circa 1.0 times body diameter in males (Fig. 39F). Each podomere with a pair of setae ventrally. Coxae 3 and beyond of cylindrical shape. Tarsus with a stout dorso-apical seta and three pairs of setae, apical pair stout, others successively smaller (Fig. 39G).

Male sexual characters: tarsal pads absent (Fig. 39G). Coxae 3 and 4 each with a short, conical coxal process. Process protruding posteriorly (Fig. 39B).

Anterior gonopod sternite elongated into a wide, almost rectangular lobe. Mesal process of coxite prominent, longer than telopodite, but shorter than telopodite process (Fig. 41A). Telopodite on anterior side with a circular opening for the posterior gonopods (Fig. 41A). Telopodite process very long, slender, slightly curved inwards. Shape resembling a sable (Fig. 41B), basally projecting to lateral side into a long, slender, well-rounded, retrorse process. Retrorse process laterally extending beyond telopodite (Fig. 41B).

Posterior gonopods unique (Figs 41C–E). Gonopod pair connected via a well-sclerotized sternite. Coxites and telopodites positioned parallel to those of opposite gonopod. Coxite wide, well-sclerotized, with a single groove (Fig. 41C). Coxite and telopodite separated by a suture. Telopodite massive, longer than and as wide as coxite (Fig. 41C). Telopodite basally divided into two branches (Figs 41D, E). Both branches of similar width and almost similar length, resembling a U (Figs 41C–E). Sperm canal protruding at base of U, running free but somehow attached to lateral main branch (Fig. 41E), tip prolonged into flagellum (Fig. 41D). Mesal branch of telopodite on anterior side medially with a finger-shaped process (Fig. 41D).

Female unknown.

Etymology: *andringitra*, noun in apposition, after the type locality, the Andringitra mountain massive.

***Alluviobolus* Wesener, gen. n.**
urn:lsid:zoobank.org:act:3190519A-4F6B-45C8-BF88-209D0E41A9C8

Type species: *Alluviobolus laticlavius*, sp. n.

Other species included:
A. tsimelahy sp. n.
A. antanosy sp. n.

Diagnosis: anterior (Fig. 44E) and posterior gonopods (Fig. 45I) uniquely shaped for Malagasy Spirobolida: mesal process of anterior gonopod coxite absent (Fig. 44E); telopodite mesally protruding into slender process (Figs 44E, G), process apically with a sharp-edged retrorse projection (Fig. 44G). Coxite and telopodite of posterior gonopods not coaxial, telopodite slightly bended posteriorly (Fig.

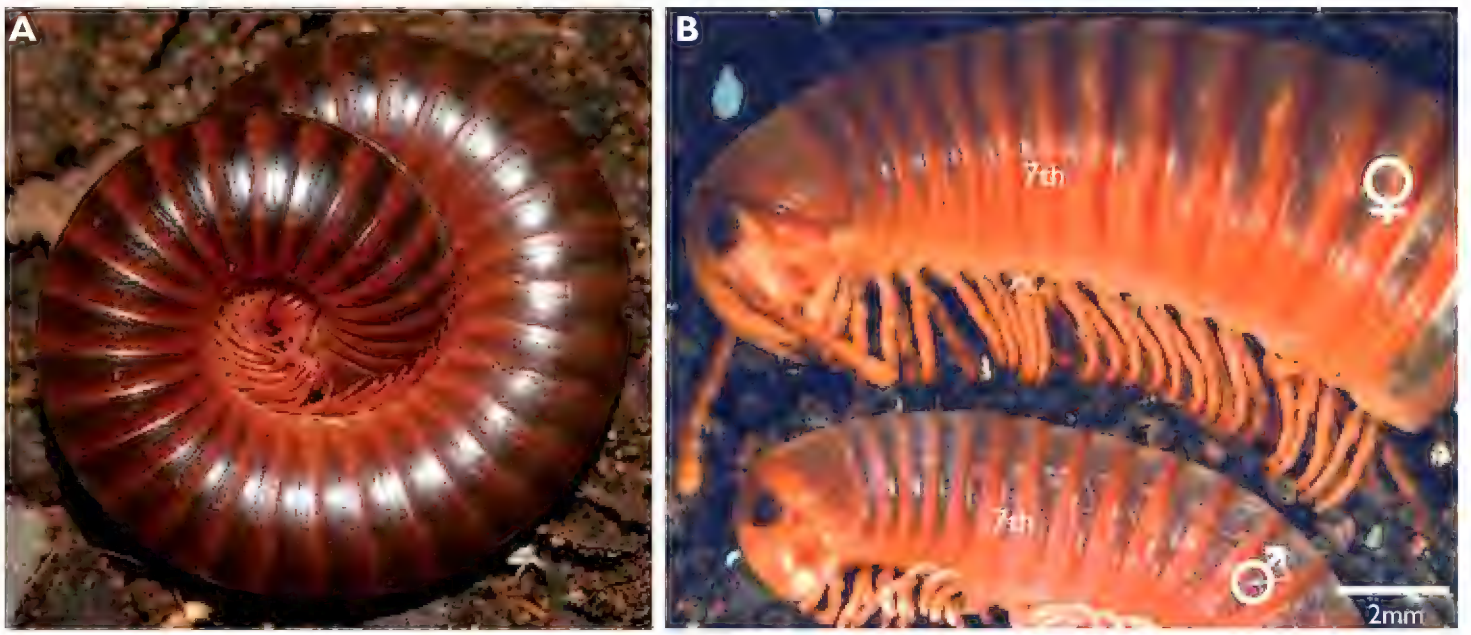

Figure 42. *Alluviobolus tsimelahy* sp. n., **A** living male from Tsimelahy **B** male and female specimen from Ebosika.

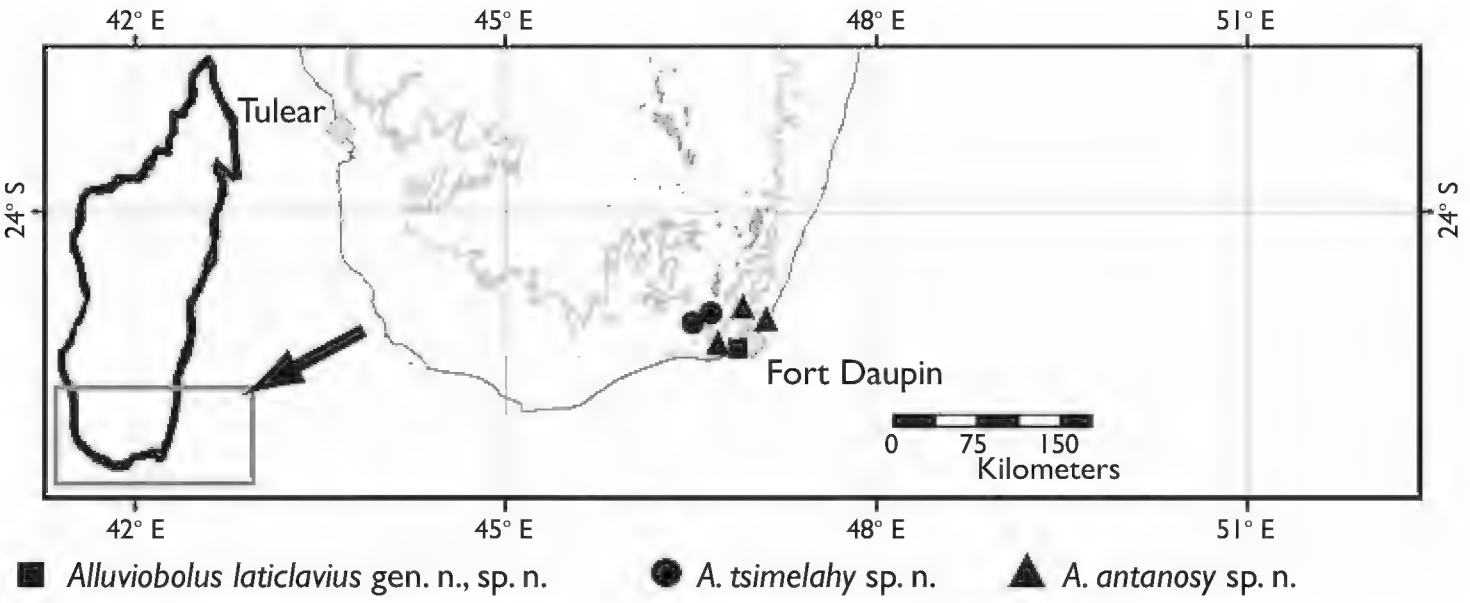

Figure 43. Distribution map of the genus *Alluviobolus* gen. n.

45I). Telopodites with a torsion, opening of sperm canal discharging apico-laterally (Figs 45I, 47G). Natural colour varies between species from brown, red to pitch-black (Figs 42A, 44C), dorsally at least on mesozonites with an orange or red stripe of species-specific width. A similar stripe is also present in *Spiromimus*, *Caprobolus* and *Ostinobolus* gen. n. species. *Alluviobolus* species share the habitus and colour pattern with species of the sympatric living genus *Ostinobolus* gen. n. Both genera, however, possess completely different anterior and posterior gonopods. Gnathochilarium with a subdivided mentum and a single sclerotized ledge on each stipites (Fig. 44D), like in *Flagellobolus*, *Riotintobolus*, *Pseudocentrobolus*, *Granitobolus*, *Caprobolus*, *Ostinobolus* **gen. n**. A torsion of the posterior gonopods (Fig. 45I) is also present in *Zehntnerobolus* (Fig. 22G) and *Riotintobolus* (Fig. 26M). A strange similarity can be observed in the posterior gonopods of *Alluviobolus* with drawings of *Trigoniulus castaneus* Attems, 1915 from New Guinea (Attems 1915: pl. I, fig. 13).

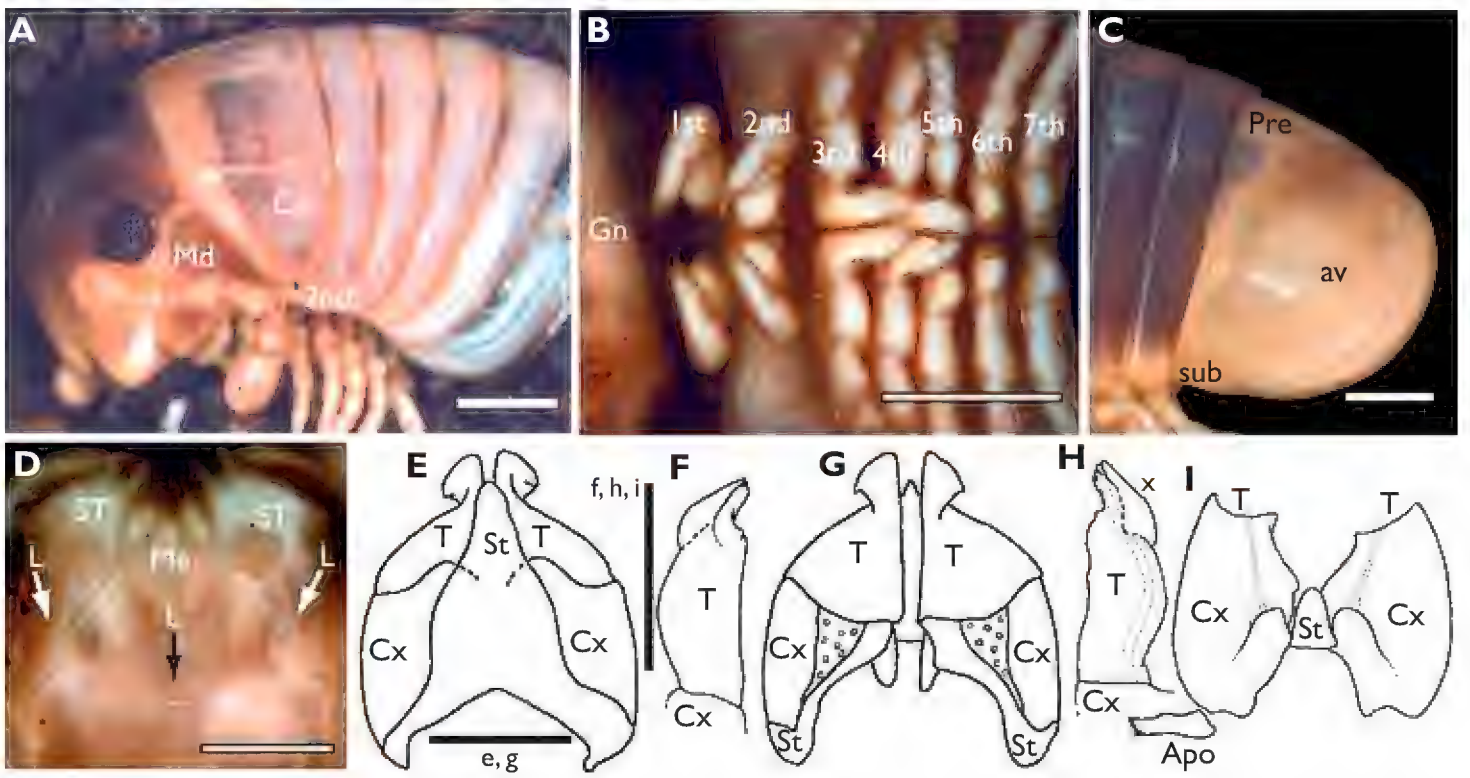

Figure 44. *Alluviobolus laticlavius* sp. n. male holotype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** gnathochilarium, ventral view **E** anterior gonopod, anterior view **F** right posterior gonopod, anterior view **G** anterior gonopod, posterior view **H** right posterior gonopod, telopodite, posterior view **I** posterior gonopods, coxite and sternite, posterior view. Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; Gn = gnathochilarium; L = ledge; Md = mandible; Me = mentum; Pre = preanal ring; St = sternite; ST = stipites; sub = subanal scale; T = telopodite. Scale bars = 1 mm.

Distribution and ecology: species of *Alluviobolus* were found in spiny, subhumid and humid forests or rainforests in southeast Madagascar (Fig. 43). The records from the spiny forest are, however, restricted to the wet alluvial of rivers and small streams, and the same species also occurs in the rainforest of Ebosika. *A. laticlavius* sp. n. occurs in the semi-dry forest of Petriky. All species of *Alluviobolus* were collected on or inside the first few centimetres of leaf litter in the forests.

Description. *Males*: length up to 47 mm, diameter up to 4.3 mm. 43–49 podous rings. Females: length up to 62 mm, diameter up to 6.0 mm. 43–49 podous rings.

Apodous rings absent in all adult specimens.

Colour species-specific. Dorsally at least on mesozonites always with a red or orange stripe.

Head: each eye with circa 22–25 ocelli arranged in 4 or 5 vertical rows (Figs 44A, 45A, 47A). Labrum with standard three irregular teeth and one row of 10–12 stout marginal setae. Clypeus with two setiferous foveolae on each side. Antennae of medium length, reaching back to ring 5 (Fig. 44A). Relative lengths of antennomeres: 1<<2=3=4=5<6 (Fig. 44A). Terminal antennomere with four large sensory cones located together inside a membranous area. Antennomere 5 latero-apically with four rows, antennomere 6 with two rows of sensilla basiconica.

Gnathochilarium unusual (Fig. 44D). Lamellae linguales each with two standard setae located behind one another. Stipites each with three apical setae. Mentum basally subdivided by a well-developed suture (Figs 46D, E). Stipites each towards mentum

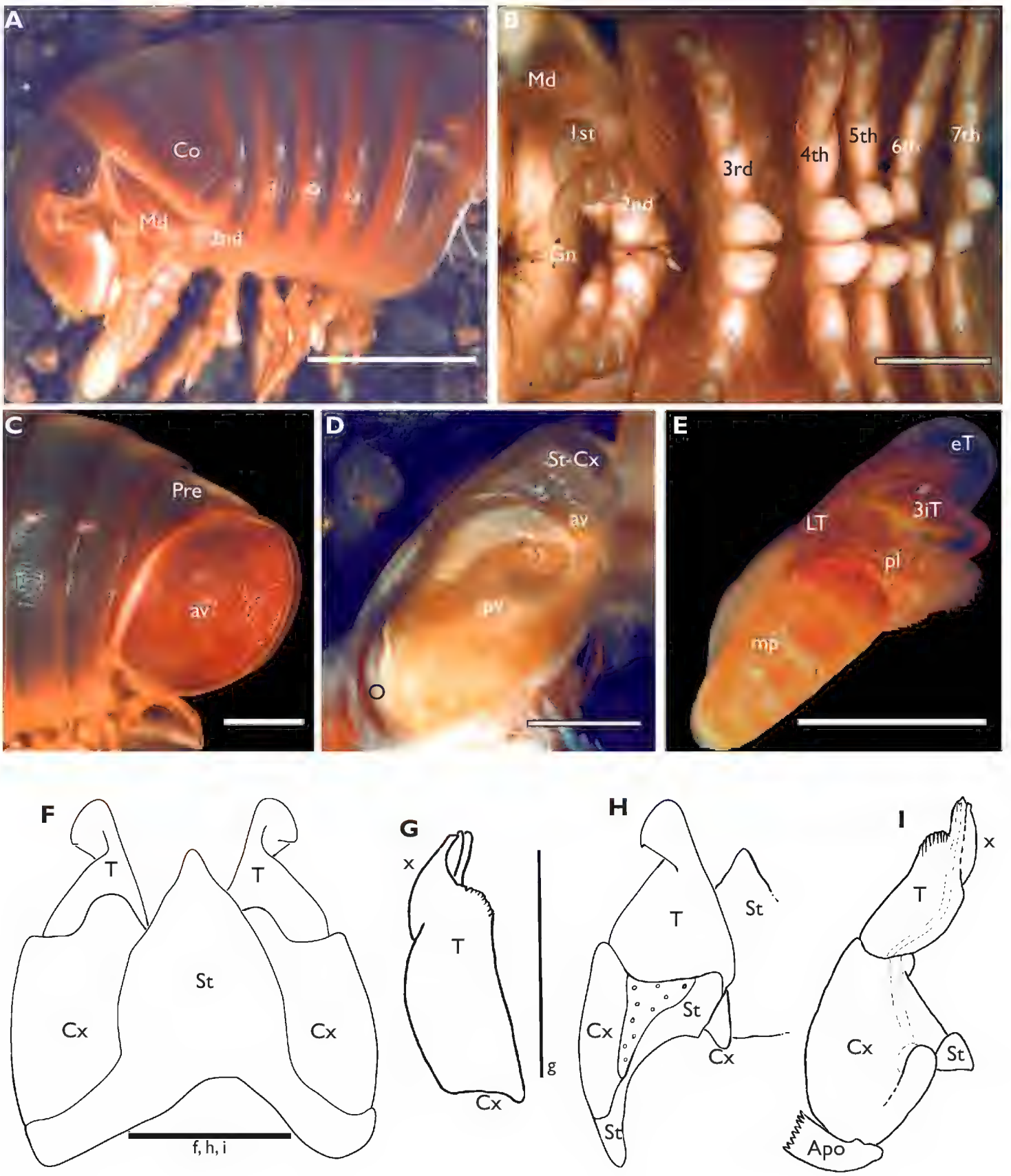

Figure 45. *Alluviobolus tsimelahy* sp. n. A–C, F–I male holotype, D, E female paratype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** vulva and sterno-coxite of second leg, posterior view **E** left mandible, mesal view **F** anterior gonopod, anterior view **G** right posterior gonopod, anterior view **H** anterior gonopod, posterior view **I** right posterior gonopod, posterior view. 3iT = 3-combed internal tooth; Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; eT = external tooth; Gn = gnathochilarium; LT = lateral tooth; Md = mandible; mp = molar plate; O = operculum; pL = pectinate lamella; Pre = preanal ring; pv = posterior valve; St = sternite; St-Cx = coxosternite; T = telopodite. Scale bars = 1 mm.

with a wide sclerotized ledge (Fig. 46E). Palpi of gnathochilarium with numerous sensilla. Hypopharyngeal crest with a field of spine-like structures (Fig. 46F). Endochilarium apically with 4–6, towards hypopharyngeal crest with >20 sensilla.

Mandible basal joints swollen (Fig. 45A). External tooth simple, rounded; mesal tooth with three cusps (Fig. 45E). Four or five pectinate lamellae. Molar plate with few (circa 5) transverse furrows, anterior three furrows greatly enlarged, posterior furrows minute (Fig. 45E).

Collum: smooth, inconspicuous. Ventrally not protruding as far as ring 2 (Fig. 45A).

Body rings: dorsally and laterally leather-like, meso- and metazona ventrally with numerous transverse impressions. Ozopores starting at ring 6, touching suture between mesozona and metazona (Figs 42A, B).

Telson: preanal process absent. Anal valves with lips and micropunctation, slightly elongated posteriorly. Subanal scale inconspicuous (Fig. 44C).

Legs: coxae 1 and 2 elongated and fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae. Length of midbody legs circa 1.1 times body diameter in males and 0.7 times body diameter in females. Each podomere with an apical, ventral seta (Figs 46G, H). Coxae 3 and beyond of cylindrical shape (Figs 46G, H). Tarsus with a stout dorso-apical seta and three pairs of ventral setae.

Male sexual characters: coxae 3–7 in some species modified (Figs 44B, 45B). Tarsal pads absent.

Anterior gonopods: median sternal projection triangular and elongated with a wide tip (Fig. 44E). Sternite always longer than coxite and telopodite, except for telopodite process. Coxite process absent. Coxite in anterior view well-visible, in posterior view only laterally present (Fig. 44G). Telopodite mesally always with a long slender process. Tip with a sharp-edged, retrorse process (Fig. 44G).

Posterior gonopods in situ almost completely covered by coxite and telopodite of anterior gonopod. Coxite and telopodite of posterior gonopod clearly divided (Figs 45I, 47G). Sternite sclerotized and well-visible (Figs 44I, 45I). Coxite mesally with a single groove. Joint protruding into a short stem towards telopodite, latter as long and wide as coxite, curved posteriorly (Fig. 45I). Telopodites arranged parallel to one another. A torsion present in telopodites, sperm canal discharging apico-laterally (Fig. 44H). Tip of telopodite mesally with a sclerite of species-specific shape (*x* in Figs 44H, 45I, 47G).

Female sexual characters: vulva simple, bivalve-like, with a small, poorly sclerotized operculum at base (Fig. 45D). Posterior valve apically overlapping part of anterior one. Basally on each valve towards opening with two or three rows of setae (Fig. 45D).

Etymology: *Alluviobolus*, masculine, Latin, consists of Alluvium referring to the alluvial of a river where large numbers of *A. tsimelahy* sp. n. could be collected, and *-bolus*.

Key to the *Alluviobolus* species:

1 Male coxae 3–7 with processes (Figs 44B, 45B). Telopodite of posterior gonopods with a sclerite of elongated triangular shape (*x* in Figs 44H, 45I). Body with 47–49 body rings..... **2**

– Male coxal processes absent (Fig. 47B). Telopodite of posterior gonopods with a sclerite of wide rectangular shape (*x* in Fig. 47G). Body with 42–44 body rings.....***A. antanosy* sp. n.**

2 Colour on mesozonites grey, metazonites black, dorsally with a wide red stripe. Male coxae 3 and 4 with slender processes (Fig. 44B). Telopodite of posterior gonopod without a lateral membranous fringe (Fig. 44H)..... ..... ***A. laticlavius* sp. n.**

– Colour on mesozonites dark green, metazonites red, dorsally on mesozonites with a slender orange stripe (Fig. 42A). Male coxae 3–5 with a large, swollen process (Figs 45B, 46B). Telopodite of posterior gonopod laterally with a membranous fringe (Figs 45I, 46L).....***A. tsimelahy* sp. n.**

***Alluviobolus laticlavius* Wesener, sp. n.**

urn:lsid:zoobank.org:act:90EB964E-EF9A-48BA-A6C3-D42741B7258E

Material examined: *Holotype:* 1 ♂ (39 mm long), FMMC 4065, Madagascar, Province Toliara, Petriky, 10 m, littoral subhumid forest, 25°3.73' S, 46°52.16' E, leg. B. L. Fisher, 22.IX.1998, sifted litter. *Paratype:* 1 ♀, FMMC, Province Toliara, Petriky, 10 m littoral forest on sand, in leaf litter, 25°03' S, 46°53' E, leg. T. Wesener, 17.IV.2003.

Differential diagnosis: the colour pattern of *A. laticlavius* is unique for *Alluviobolus* and also for millipedes living in Petriky, allowing a secure identification of this species. *A. laticlavius* differs from *A. antanosy* sp. n. in the shape of posterior gonopods and male coxal processes, although the latter species can be found just five kilometers south of Petriky. The posterior gonopods of *Alluviobolus laticlavius* are quite similar to those of *A. tsimelahy* sp. n. *A. laticlavius*, however, differs from the latter in the shape of the male coxal processes as well as in the colour pattern.

Description. holotype with 47 body rings, 39 mm long, 3.9 mm wide.

Coloration on mesozonites faded to grey, metazonites black (Fig. 44C). Rings dorsally with a wide red stripe. Legs, antennae, anal valves, subanal scale and posterior part of preanal process faded to light brown (Figs 44A–C). *Eyes* with circa 25 ocelli arranged in five rows (Fig. 44A). *Antennae* protruding back to ring 5 (Fig. 44A). *Male coxal processes* only present on coxae 3 and 4 (Fig. 57B). Processes slender, bended posteriorly and protruding above coxa of adjacent leg. *Preanal process* absent (Fig. 44C).

Anterior gonopod sternite elevated into a wide lobe, apically slightly tapering. Tip well-rounded (Fig. 44E). Coxite and telopodite inconspicuous (Figs 44E, G).

Posterior gonopods: telopodite without a membranous fringe (Fig. 44H). Apical sclerite (*x* in Fig. 44H) slender, triangular, regularly protruding into a slender, acute tip (Fig. 44F).

Distribution and ecology: this species is only known and possibly microendemic to the worldwide unique (Vincelette et al. 2003) subhumid littoral forest of Petriky (Fig. 43). Like other species of the genus, does *A. laticlavius* lives on and in the leaf litter.

Etymology: *laticlavius*, adjective, refers to the characteristic wide red stripe of this species.

Alluviobolus tsimelahy Wesener, sp. n.

urn:lsid:zoobank.org:act:EA739EC9-0459-4440-891A-6D703BDE2FCC

Material examined: 14 ♂, 21 ♀, 47 imm. *Holotype:* 1 ♂ (42 mm long), FMMC W017D, Madagascar, Province Toliara, RNI Andohahela, parcel II, Tsimelahy, gallery forest, in alluvial debris, 24°57.296' S, 46°37.214' E, leg. T. Wesener et al., 24.V.2007. *Paratypes:* 4 ♂, 6 ♀, 6 imm., FMMC W017D, same data as holotype; 1 ♂, 1 ♀, 2 imm., CAS W017D, same data as holotype; 1 ♂, 1 ♀, ZMUC W017D; 1 ♂, 1 ♀, ZMH W017D, same data as holotype.

Other material examined: 4 ♂, 4 ♀, 10 imm., W017D, same data as type material, but stored as vouchers at University Antananarivo; 1 ♂, 4 ♀, 9 imm., FMMC W016A, Andohahela mountain chain, Ebosika, rainforest, 24°56'45.24" S, 46°40'31.84" E, leg. T. Wesener et al., 15.VI.2007; 1 ♂, 4 ♀, 9 imm., W016A, same data as previous, University Antananarivo.

Differential diagnosis: see *A. laticlavius* for a differentiation of both taxa. It is possible that *Ostinobolus rufus* sp. n. can also be found in the Ebosika rainforest. Both species live in the same habitat and are of similar size and colour. *O. rufus* is, however, entirely red (Fig. 48C) while the mesozonites are dark olive greenish in *Alluviobolus tsimelahy* (Fig. 42A).

Description. *Measurements*: males with 47–49 body rings, circa 41–44 mm long, 3.6–4.3 mm wide. Females with 47–49 body rings, 52–60 mm long, 5.5–6.0 mm wide.

Coloration on mesozonites dark olive green, metazonites red (Fig. 42A). Rings dorsally with a slender orange stripe. Head, legs, antennae and telson red (Figs 45A–C). *Eyes* with 22–24 ocelli arranged in 4 or 5 rows (Fig. 45A). *Antennae* protruding back to ring 5 (Fig. 45A).

Male coxal processes on coxae 3–5 (Fig. 45B), 3 and 4 large, swollen, process on coxa 5 smaller (Fig. 46B). *Preanal process* absent (Figs 45C, 46C).

Anterior gonopod sternite elevated into a wide lobe, apically tapering. Tip well-rounded (Fig. 45F). Coxite and telopodite inconspicuous (Fig. 45H).

Posterior gonopods: telopodite with a membranous fringe (Fig. 45I). Apical sclerite (*x* in Fig. 45I) slender, triangular, regularly protruding into a slender, acute tip (Fig. 45G).

Intraspecific variation: specimens from the rainforest of Ebosika show minute differences in the posterior gonopods towards those of the type series (compare Figs

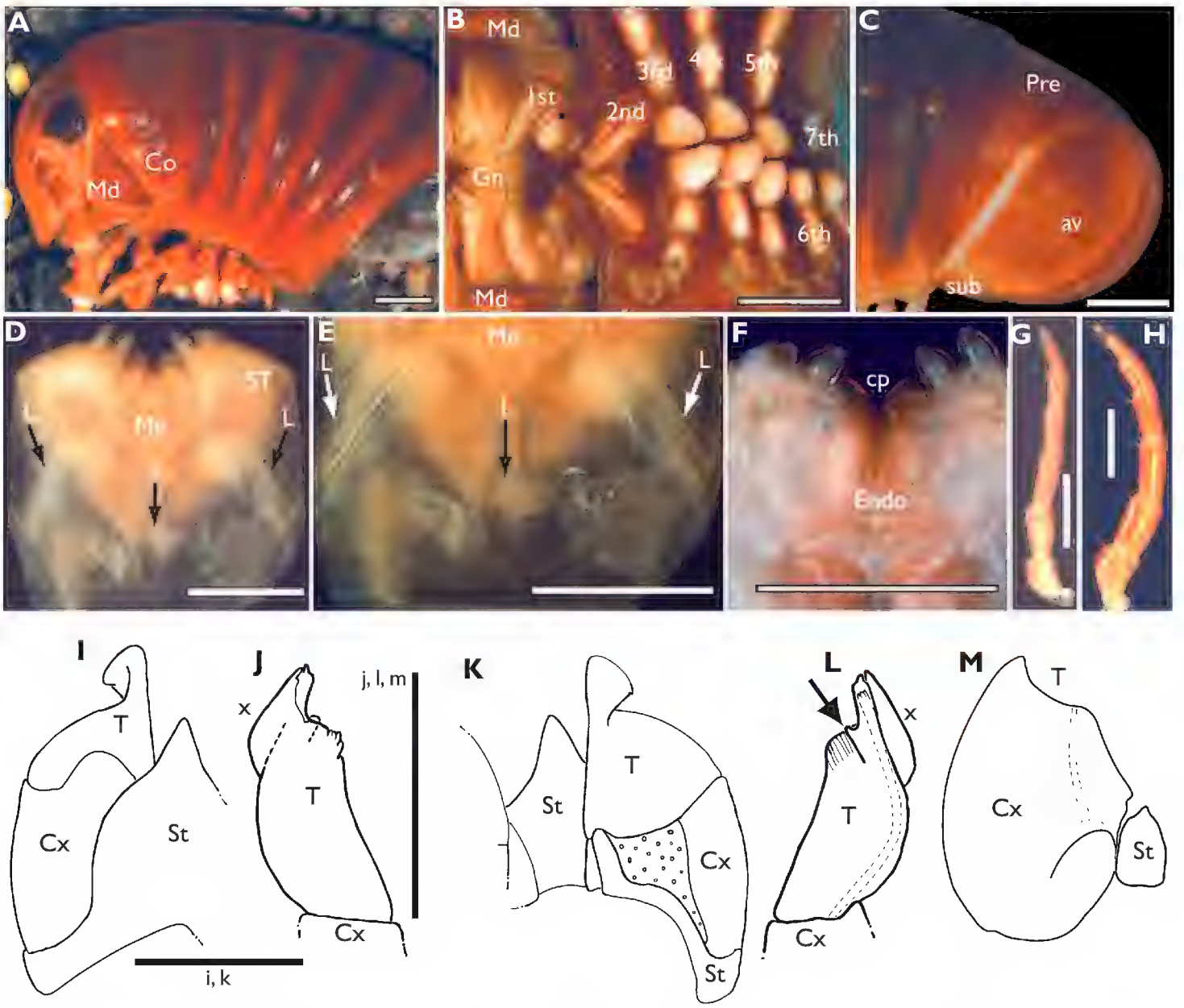

Figure 46. *Alluviobolus tsimelahy* sp. n. specimens from Ebosika, A–G, I–M male, H female. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** gnathochilarium, ventral view **E** gnathochilarium, mentum **F** gnathochilarium, dorsal view on endochilarium **G, H** left midbody legs **I** anterior gonopod, anterior view **J** right posterior gonopod, anterior view **K** anterior gonopod, posterior view **L** right posterior gonopod, telopodite, posterior view **M** right posterior gonopods, coxite and sternite, posterior view. Apo = apodeme; av = anal valves; Co = collum; cp = central pads; Cx = coxite; Endo = endochilarium; Gn = gnathochilarium; L = ledge; Md = mandible; Me = mentum; Pre = preanal ring; St = sternite; ST = stipites; sub = subanal scale; T = telopodite. Scale bars = 1 mm.

45G, I with Figs 46J, L, M). Ebosika specimens possess apically on the telopodite a short protruding process towards the membranous fringe (Fig. 46L, marked with an arrow). However, size, number of body rings, colour pattern and the shape of male coxal processes (Figs 46A–C) are identical in specimens from both populations.

Distribution and ecology: *A. tsimelahy* is until now the only known Malagasy species of Spirobolida which occurs in the spiny forest and rainforest ecosystem, more precisely in the spiny forest at Tsimelahy and just 5 km east in the rainforest of Ebosika. The record from the spiny forest of Tsimelahy, however, is tainted, because the only place where *Alluviobolus* specimens were found was very close to the river, inside wet debris. It is currently unknown if the *A. tsimelahy* specimens from the spiny forest area represent

a stable population or whether specimens just floated out of the rainforest and into the spiny forest during the wet season. It is perhaps not a coincident that the specimens from Ebosika were collected close to the same river as those in Tsimelahy (Fig. 43).

Etymology: *tsimelahy*, noun in apposition, after the type locality.

***Alluviobolus antanosy* Wesener, sp. n.**
urn:lsid:zoobank.org:act:1AAC85EB-6256-450E-B461-707D235E61BA

Material examined: 5 ♂, 7 ♀, 4 imm Holotype: 1 ♂ (45 mm long), FMMC W100A, Madagascar, Province Toliara, Ambatotsirongorongo Mountain, Grand Lavasoa, 25°5'10.23" S, 46°44'55.93" E, rainforest, leg. T. Wesener et al., 14.IV.2007. *Paratypes:* 1 ♂, 1 F., FMMC W100A, same data as previous; 1 ♂, FMMC, Province Toliara, Sainte Luce, S9, littoral forest on sand, 24°47' S, 47°10' E, leg. T. Wesener, 06.IV.2003; 1 ♂, FMMC 13608, Province Toliara, Esetra, Mt. Mahermana, 340 m, station 1, summit, 0° slope, frequent granite outcrops, 24°26'12" S, 47°13'13" E, leg. K. Emberton, 25.I.1995; 1 ♂, 2 ♀, FMMC W049A, Andohahela I, Isaka-Ivondro Sud, rainforest, 24°49.690' S, 46°51.971' E, leg. T. Wesener et al., 08.VI.2007; 1 ♀, ZMH W049A; same data as previous; 1 ♀, ZMUC W049A, same data as previous.

Other material examined: 2 ♀, 4 imm., W049A, same data as previous, but stored as vouchers at University Antananarivo.

Differential diagnosis: *A. antanosy* differs from all congeners in the absence of male coxal processes (Fig. 47B). While the anterior gonopods are very similar in all species of the *Alluviobolus* (Figs 47D, F), are the posterior gonopods in *A. antanosy* rectangular apically (Fig. 47G), compared with acute telopodite tips in *A. laticlavius* (Fig. 44H) and in *A. tsimelahy* (Fig. 46L).

Description. *Measurements*: males with 42–44 body rings, circa 43–47 mm long, 3.2–3.8 mm wide. Females with 43 or 44 body rings, 54–62 mm long, 5.0–5.5 mm wide.

Coloration on mesozonites dark grey, metazonites red (Fig. 47C). Rings dorsally with a slender orange stripe. Head, legs, and posterior part of telson red (Figs 47A–C). Antennae and anterior part of telson dark grey (Figs 47A, C). *Eyes* with 22–25 ocelli arranged in 4 or 5 rows (Fig. 47A). *Antennae* protruding back to ring 5 (Fig. 47A). *Male coxal processes* absent, coxa 3 of slightly conical shape (Fig. 47B). *Preanal process* absent (Fig. 47C)

Anterior gonopod sternite elevated into a broad triangular lobe. Tip well-rounded (Fig. 47D). Coxite and telopodite inconspicuous (Fig. 47F).

Posterior gonopods: telopodite membranous fringe absent (Fig. 47E). Apical sclerite (*x* in Fig. 47G) wide, rectangular. Tip broadly rounded, basally elongated to a thin spine (Fig. 47E).

Distribution and ecology: widely distributed in rainforests of Southeastern Madagascar. *A. antanosy* was collected in the Andohahela and Vohimena mountain chain as well as in the lowland littoral rainforest of Sainte Luce and the isolated Ambatotsirongorongo Mountain (Fig. 43). All specimens were found on the soil surface.

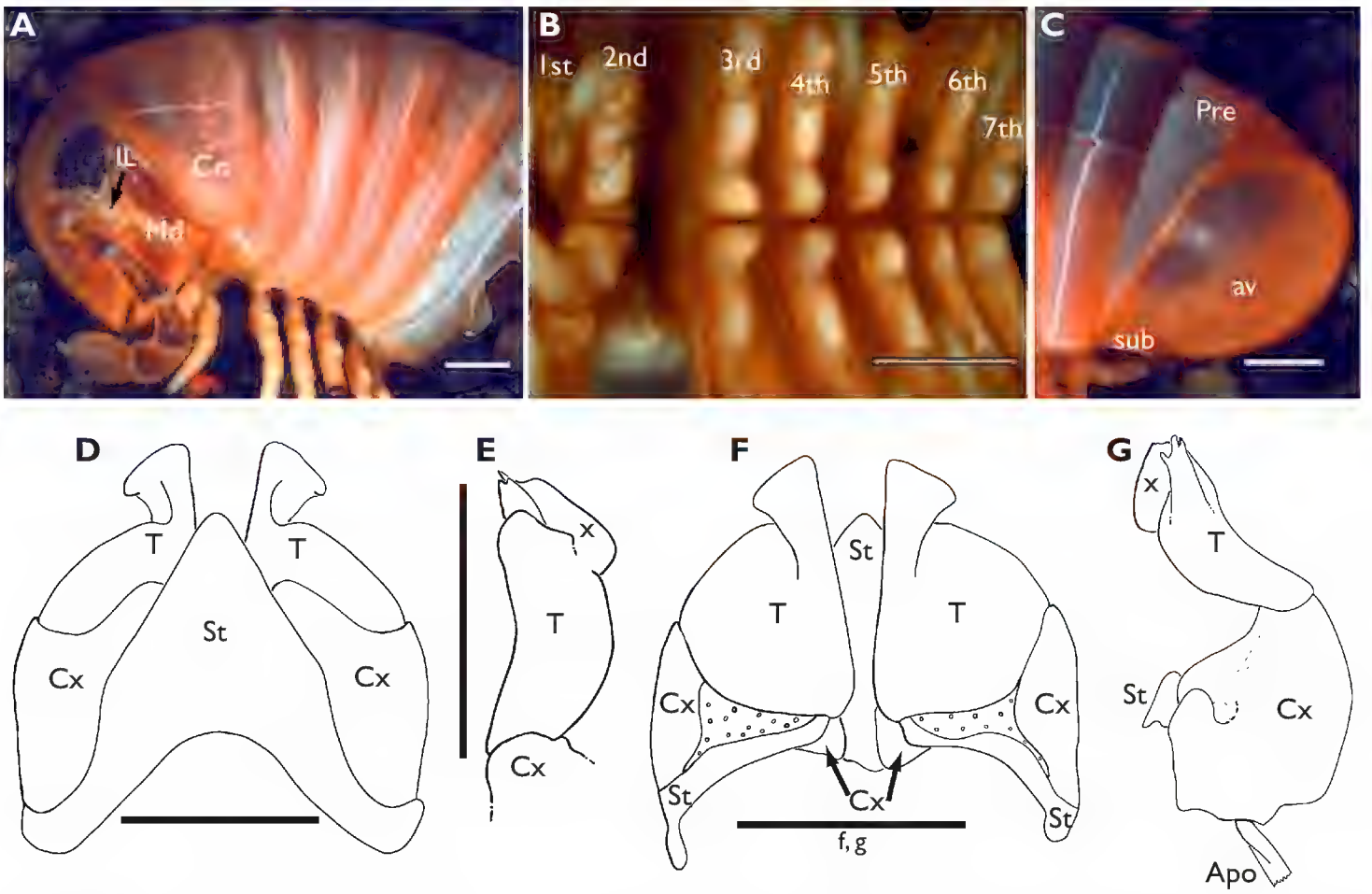

Figure 47. *Alluviobolus antanosy* sp. n., male holotype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** anterior gonopod, anterior view **E** left posterior gonopod, anterior view **F** anterior gonopod, posterior view **G** left posterior gonopod, posterior view. Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; IL = incisura lateralis; Md = mandible; Pre = preanal ring; St = sternite; sub = subanal scale; T = telopodite. Scale bars = 1 mm.

Etymology: *antanosy*, noun in apposition, after the Malagasy Antanosy people, who live around Tolagnaro (Fort Dauphin) where this species was collected.

***Ostinobolus* Wesener, gen. n.**
urn:lsid:zoobank.org:act:1A0ECD32-48CB-4631-AE39-06263DF7EB87

Type species: *Ostinobolus rufus* sp. n.

Other species included:
O. stellaris sp. n.
O. montanus sp. n.
O. subterraneus sp. n.

Diagnosis: the posterior gonopods of *Ostinobolus* with their apically swollen membranous area (*v* in Figs 48J, 50F, 51G, 52H) are unique among Spirobolida. Telopodites of anterior gonopod diverse, either inconspicuous (Fig. 51F), or on posterior side apically with a small, non-protruding process (Fig. 48H), or with a large retrorse

Figure 48. *Ostinobolus rufus* sp. n., A, B, D, G–J male holotype; C, E, F male paratype. **A** head, lateral view **B** legs 1–7, ventral view **C** living specimen **D** telson **E** gnathochilarium **F** midbody ring with leg **G** anterior gonopod, anterior view **H** anterior gonopod, posterior view **I** left posterior gonopod, anterior view **J** left posterior gonopod, posterior view. Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; Gn = gnathochilarium; L = ledge; Md = mandible; Pre = preanal ring; St = sternite; sub = subanal scale; T = telopodite. Scale bars = 1 mm.

process (Fig. 52G). Telopodites of posterior gonopod as wide as coxites, arranged face-to-face with one another. First leg pair longer than second (Fig. 52A). Living specimens roll themselves into a double-spiral when disturbed. Natural colour varies between species, red to brown (Figs 48A, C, 52A, C). Some *Ostinobolus* species share the habitus and the colour pattern with species of the sympatric living *Alluviobolus*. The latter, however, differs from the former in the presence of completely different anterior and posterior gonopods. Gnathochilarium with a subdivided mentum and a single sclerotized ledge on each stipites (Figs 48E, 52D), like in *Flagellobolus*, *Riotintobolus*, *Pseudocentrobolus*, *Granitobolus*, *Caprobolus*, *Alluviobolus*. Species of this genus share fewer characters on the anterior gonopods than other genera of Spirobolida. Especially the placement of the unusual *O. subterraneus* sp. n. inside *Ostinobolus* is tentative at best.

Distribution and ecology: species of *Ostinobolus* could be recorded with four species from the rain- and subhumid forests in Southeastern Madagascar (Fig. 49). Most species are restricted to the rainforest and littoral rainforest with the exception of *O. subterraneus* sp. n. which also occurs in the semi-dry forest of Petriky. Specimens of *O. rufus* sp. n. were always collected on the soil surface, with juveniles feeding 1–2 cm deeper in the leaf litter. The same life style can be suggested for *O. stellaris* sp. n. and *O. montanus* sp. n., which share a similar colour pattern and leg length with *O. rufus* sp. n. *O. subterraneus* sp. n., however, differs from the other species of the genus in living deeply inside the root horizon of the soil.

Description. *Males*: length up to 53 mm, diameter up to 4.4 mm. 40–49 podous rings. Female length up to 65 mm, diameter up to 6.3 mm. 40–48 podous rings.

Colour highly species-specific, see species descriptions.

Head: each eye with circa 20–25 ocelli arranged in 4–6 vertical rows (Figs 48A, 50A, 51A). *O. subterraneus* sp. n. with only 6–8 decolorized and fused ocelli (Fig. 52A). Labrum with standard three irregular teeth and a row of 10–12 stout marginal setae. Clypeus with two setiferous foveolae on each side. Antennae of medium length, reaching back to ring 3–5 (Fig. 51B). Relative lengths of antennomeres: 1<<2=3=4=5<6

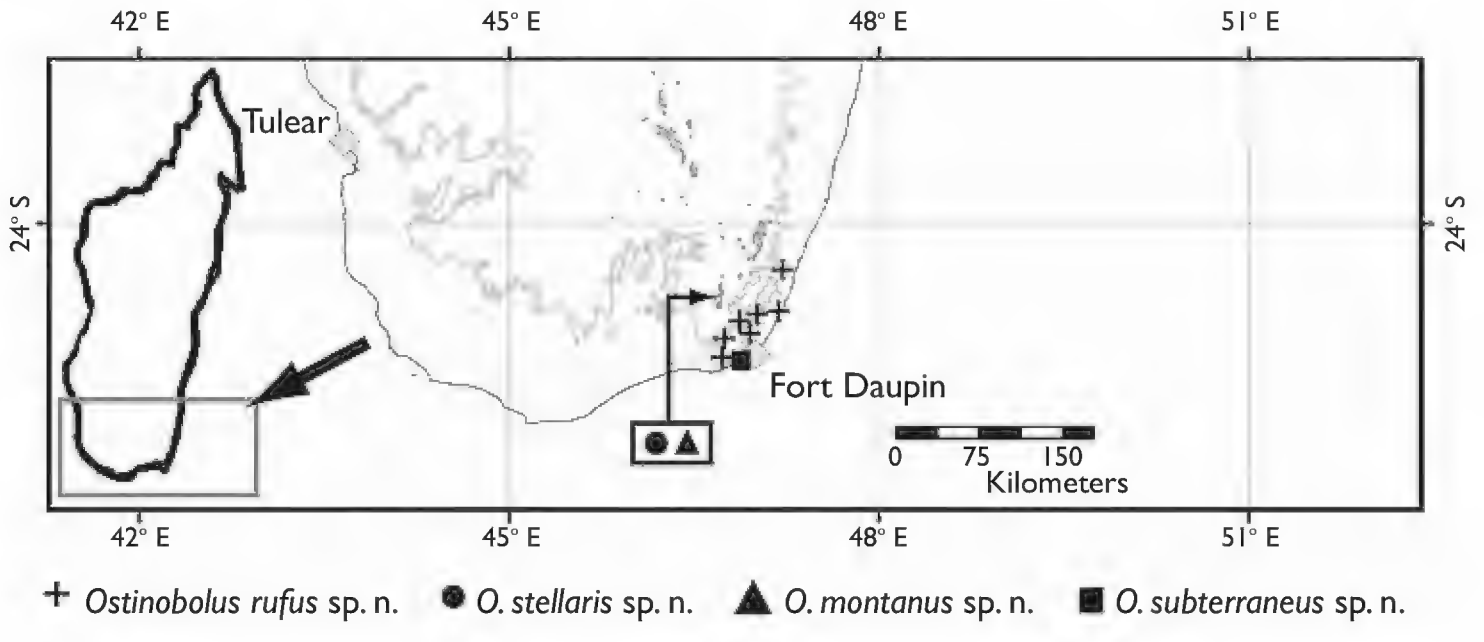

Figure 49. Distribution map of the genus *Ostinobolus* gen. n..

(Fig. 48A). Terminal antennomere with four large sensory cones located together inside a membranous area. Antennomere 5 apically with four rows, antennomere 6 with two rows of sensilla basiconica.

Gnathochilarium unusual (Fig. 48E). Lamellae linguales each with two standard setae located behind one another. Stipites each with three apical setae. Mentum basally subdivided by a conspicuous suture (Figs 48E, 52D). Stipites towards mentum with a wide sclerotized ledge (Fig. 48E). Hypopharyngeal crest with a field of spine-like structures. Number of sensilla on central pads not counted.

Mandible: external tooth simple, rounded; mesal tooth with three cusps. Six pectinate lamellae. Molar plate with few (6 or 7) transverse furrows, anterior three furrows enlarged, posterior furrows minute.

Collum: smooth, laterally not protruding as far as body ring 2 (Fig. 48A).

Body rings: dorsally and laterally smooth, meso- and metazona ventrally with numerous transverse impressions. Ozopores starting at ring 6, touching suture between mesozona and metazona (Fig. 48C).

Telson: preanal process absent. Anal valves with neither lips, nor grooves, nor micropunctation, but posteriorly elongated. Subanal scale inconspicuous (Figs 48D, 50C, 51C).

Legs: coxae 1 and 2 elongated and fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae. First leg pair longer than second (Fig. 52A). Tarsus 2 with only small claw, but 3–6 ventral spines. Length of midbody legs (with exception of *O. subterraneus* where leg length is reduced) circa 1.2 times body diameter in males (Fig. 48F) and 0.8 times body diameter in females. Each podomere with an apical, ventral seta. Coxae 3 and beyond of cylindrical shape (Fig. 48F). Tarsus with a stout dorso-apical seta and five pairs of ventral setae.

Male sexual characters: coxae 3 and 4 in some species elongated into short cylindrical cone (Figs 48B, 51B).

Anterior gonopods: median sternal projection triangular, with a wide, well-rounded tip (Fig. 48G). Sternite in most species longer than coxite. Coxite without a process, in anterior view well-visible, in posterior view only laterally present (Figs 48H, 51F). Telopodite diverse inside the genus, see species-specific descriptions.

Posterior gonopods in situ almost completely covered by anterior gonopod coxite and telopodite. Posterior gonopods coxite and telopodite completely fused, but suture partly visible (Fig. 48J). Sternite sclerotized and well-visible (Fig. 48J). Coxite protruding into a short stem towards telopodite, basally with a single spermatic groove. Telopodite as long and as wide as coxite (Fig. 48J), the former arranged face-to-face with one another. Shape of telopodite species-specific, but apically always with a large, swollen membranous area (*v* in Figs 48J, 50F, 51G, 52H). Sperm canal discharging mesally, basal to membranous area (*w* in Figs 48J, 50F, 51G, 52H).

Female sexual characters: vulva simple, bivalve-like, with a small, poorly sclerotized operculum at base. Posterior valve apically overlapping anterior one, both smooth, sensory cones absent. Towards opening, basally on each valve are two or three rows of setae.

Etymology: *Ostinobolus*, masculine, consists of *Ostino-* referring to the superficial resemblance of the posterior gonopods to a human femur bone, and *-bolus*.

Key to the *Ostinobolus* species:

1 Telopodite of posterior gonopods apically expanded into a star-shaped wider area (Figs 48J, 50E). Sperm canal discharging into a membranous fringe (*w* in Figs 48J, 50F) apically on telopodite **2**

– Telopodite of posterior gonopods never expanded into a star-shaped area (Figs 51E, 52F). Sperm canal protruding mesally above telopodite; never developed as a membranous fringe (*w* in Figs 51E, 52H) **3**

2 Specimens with 46–49 body rings. Sternite of anterior gonopod elongated into a slender, rectangular lobe (Fig. 48G). Telopodite of anterior gonopods in posterior view with an apical swollen process. Telopodite of posterior gonopod 3.6 times longer than wide (Fig. 48J), apically with a membranous fringe (*w*) and a membranous process (*x*) ..... ***O. rufus* sp. n.**

– Specimens with 40 body rings. Sternite of anterior gonopod wide and broadly rounded (Fig. 50D). No processes on telopodite of anterior gonopod. Telopodite of posterior gonopod 2.5 times longer than wide (Fig. 50E), apically with an additional process between membranous fringe (*w*) and membranous process (*x*, Figs 50E, G) ..... ***O. stellaris* sp. n.**

3 Eyes with circa 25 black ocelli (Fig. 51A). Colour with traces of red (Fig. 51C). Specimens 45–52 mm long, with 39 or 40 body rings. Male coxae 3 and 4 with a short, cylindrical process (Fig. 51B). Male legs long, 1.1 times body diameter. No processes on anterior gonopod telopodite (Fig. 51F). Posterior gonopod slender, slightly curved inwards. Width of telopodite only slightly increasing towards apex (Fig. 51G) ..... ***O. montanus* sp. n.**

– Eyes reduced, with only 8 decolorized ocelli (Fig. 52A). Colour brownish-greyish (Fig. 52C). Specimens 28–32 mm long, with 42–44 body rings. Male coxae unmodified (Fig. 52B). Male legs very short, 0.4 times body diameter. Anterior gonopod telopodite with a large retrorse process (Fig. 52G). Posterior gonopod running straight, short and relatively wide ..... ***O. subterraneus* sp. n.**

***Ostinobolus rufus* Wesener, sp. n.**
urn:lsid:zoobank.org:act:4F757E14-FDBD-424D-AC84-F845D06D5C46

Material examined: 47 ♂, 71 ♀, 112 imm. *Holotype:* 1 ♂ (50 mm long, dissected), FMMC W042A, Madagascar, Andohahela, Malio, rainforest, 24°55.810' S, 46°46.343' E, leg. Wesener et al., 30.V.2007. *Paratypes:* 6 ♂, 8 ♀, 13 imm., FMMC W042A, same data as holotype; 1 ♂, 1 ♀, 2 imm., CAS W042A, same data as holotype; 1 ♂, 1 ♀, 2 imm., ZMH W042A, same data as holotype.

Other material examined: 6 ♂, 10 ♀, 18 imm., W042A, same data as type material, University Antananarivo; 1 ♂, 3 ♀, 2 imm., FMMC W009A, Ambatotsirongorongo Mountain, Petit Lavasoa, 668 m, rainforest, 25°05.021' S, 46°46.110' E,

leg. Wesener et al., 21.V.2007; 3 ♀, 2 imm., W009A, same data as previous, University Antananarivo; 2 ♂, 2 ♀, 6 imm., FMMC W028A, Sainte Luce, S9, 12 m, littoral forest on sand, 24°46.769' S, 47°10.288' E, leg. Wesener et al., 01.VI.2007; 2 ♂, 2 ♀, 6 imm., W028A, same data as previous, University Antananarivo; 1 ♂, 2 ♀, 14 imm., FMMC W050A, Andohahela, Isaka-Ivondro Sud, 46 m, rainforest, 24°49.690' S, 46°51.971' E, leg. Wesener et al., 08.VI.2007; 2 ♀, 14 imm., W050A, same data as previous, University Antananarivo; 4 ♂, 5 ♀, 5 imm., FMMC W080, Manantantely, rainforest, 24°59'17.14" S, 46°55'27.95" E, leg. Wesener et al., 06.VI.2007; 4 ♂, 4 ♀, 6 imm., W080, same data as previous, University Antananarivo; 4 ♂, 3 ♀, 8 imm., FMMC W086, Ivorona, 114 m, rainforest, 24°50.026' S, 46°56.943' E, leg. Wesener et al., 23.V.2007; 1 ♂, 1 ♀, ZMUC W086, same data as previous; 5 ♂, 3 ♀, 7 imm., W086, same data as previous, University Antananarivo; 1 ♂, 2 ♀, 5 imm., FMMC W100, Ambatotsirongorongo Mountain, Grand Lavasoa, rainforest, 25°5'10.23" S, 46°44'55.93" E, leg. Wesener et al., 14.VI.2007; 2 ♀, 8 imm., W100, same data as previous, University Antananarivo; 1 ♂, 4 W, FMMC, Sainte Luce, littoral forest on sandy soil, 24°47' S, 47°10'E, leg. T. Wesener, 06.IV.2003, ex wet leaf litter; 1 ♂, FMMC 6B TIM, Vohimena Mountains, Mt. Illapiry, 500 m, station 6, on ridge w/20° slope, E of summit, some granite outcrops, 24°51'33" S, 47°00'27" E, leg. K. Emberton, 31.I.1995; 3 ♂, 1 ♀, FMMC 13602, Andohahela, Vasiha, slope 15°E, 24°55'19" S, 46°44'45" E, leg. K. Emberton, 6.II.1995; 1 ♂, FMMC 13607, Vohimena Mountains, Mt. Illapiry, 400 m, station 7, on 45° slope, SSE of summit, many granite outcrops, 24°51'27" S, 47°00'38" E, leg. K. Emberton, 31.I.1995; 1 ♀, FMMC 13606, same data as previous; 1 ♂, FMMC 13608, Esetra, Mt. Mahermana, 340 m, station 1, summit, 0° slope, frequent granite outcrops, 24°26'12" S, 47°13'13" E, leg. K. Emberton, 25.I.1995; 1 ♀, FMMC 13605, same data as previous.

Differential diagnosis: *Ostinobolus rufus* shares the star-like tip of the posterior gonopod (Fig. 48J) only with *O. stellaris* sp. n. The former differs from the latter in the higher number of body rings, differences in the anterior and posterior gonopods including a conspicuous longer posterior gonopod in *O. rufus* than in *O. stellaris* sp. n.

Description. *Measurements*: males with 46–49 rings, 43–53 mm long, 3.8–4.4 mm wide. Females with 46–48 rings, 56–65 mm long, 5.5–6.3 mm wide.

Coloration red (Figs 48A–D). Rings dorsally with an irregular yellow stripe. Mesozonites and part of metazonites between stripe and opening of ozopores darker blackish (Fig. 48C).

Eyes with circa 25 ocelli arranged in five rows (Fig. 48A). *Antennae* protruding back to ring 5 (Fig. 48A). *Male coxal processes* only on coxae 3 and 4, short and conical. Prefemur 3–5 with hollow invaginations (Fig. 48B). *Preanal process* absent (Fig. 48D).

Anterior gonopod sternite basally wide, apically elevated into a lobe with a slender, rectangular tip (Fig. 48G). Sternite tip almost as high as telopodite. Coxite not extending beyond sternite, inconspicuous (Fig. 48H). Telopodite on posterior side apically with a small, erect process. Process not projecting above telopodite margins (Fig. 48H).

Posterior gonopods: basal stem of telopodite 3.6 times longer than wide (Fig. 48J). Apical part of telopodite star-shaped (Fig. 48I). At mesal margin with three star arms

(*x*, *y*, *z* in Fig. 48J). Telopodite apically with a small membranous process (*x* in Fig. 48I) and a well-developed membranous fringe (*w*).

Intraspecific variation: although specimens were collected from no less than nine localities, spread over rainforest in the whole southeastern region of Madagascar (Fig. 49), no intraspecific variation was observed. The numbers of rings varied within the same population as much as between populations. Females are always larger and thicker than males.

Distribution and ecology: this species could be recorded from each single inventoried rainforest south of the Andohahela Isaka-Ivondro corridor (Fig. 49). It was not found (yet?) in the highly endangered (Vincelette et al. 2003) littoral forest of Mandena.

Etymology: *rufus*, adjective, refers to the characteristic red colour pattern.

***Ostinobolus stellaris* Wesener, sp. n.**

urn:lsid:zoobank.org:act:CF18E6B2-0F2E-42C8-ACF7-B5D8654FA29D

Material examined: *Holotype:* 1 ♂ (37 mm long), FMMC 8198, Madagascar, Province Toliara, RNI Andohahela, parcel I, camp 3, 1200 m, rainforest, 24°35.0' S, 46°44.1' E, leg. S. Goodman, 7–17.XI.1995, pitfall traps.

Differential diagnosis: *O. montanus* sp. n. is slightly larger than *O. stellaris*, the former differs from the latter in the presence of male coxal processes (Fig. 51B) and completely different shaped posterior gonopods (Fig. 51G). See above for a separation of *O. stellaris* and *O. rufus*.

Description. *Measurements*: male holotype with 40 rings, circa 37 mm long (broken), 3.7 mm wide.

Coloration faded in alcohol. Antennae and legs reddish, with white tips (Fig. 50A). Head, collum, median part of body rings and telson greyish (Fig. 50C). Metazona of body rings red. *Eyes* with circa 25 ocelli arranged in five rows (Fig. 50A).

Antennae protruding back to ring 5 (Fig. 50A).

Male coxal processes absent, but width of coxae 3 and 4 enlarged (Fig. 50B). *Preanal process* absent (Fig. 50C).

Anterior gonopod sternite lobe wide, broadly rounded (Fig. 50D). Sternite tip lower than coxite. Coxite and telopodite inconspicuous, processes absent (Fig. 50D).

Posterior gonopods: basal stem of telopodite elongated, 2.5 times longer than wide (Fig. 50E). Apical part of telopodite star-shaped (Fig. 50F). At mesal margin with three star arms (*x*, *y*, *z* in Fig. 50E). Telopodite apically with a small membranous process (*x* in Fig. 50F) and a well-developed membranous fringe (*w*). Between fringe (*w*) and membranous process (*x*) with a second process (Figs 50E, F).

Distribution and ecology: only known from the Anosy rainforest north of the Isaka-Ivondro corridor (Fig. 49).

Etymology: *stellaris*, adjective, refers to the star-like shape of the posterior gonopod telopodite.

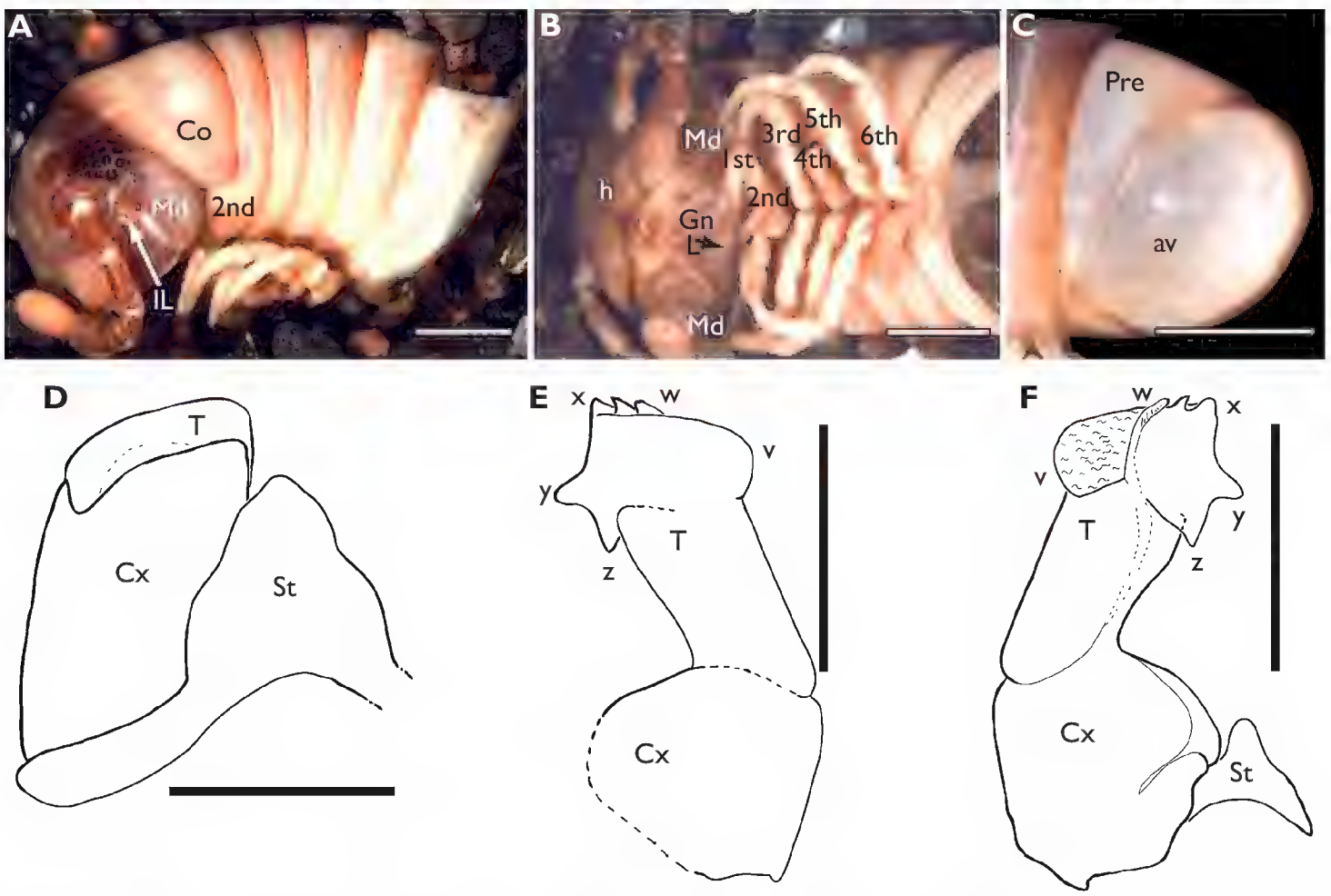

Figure 50. *Ostinobolus stellaris* sp. n., male holotype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** anterior gonopod, anterior view **E** right posterior gonopod, anterior view; **F**: right posterior gonopod, posterior view. av = anal valves; Co = collum; Cx = coxite; Gn = gnathochilarium; h = head; IL = incisura lateralis; L = ledge; Md = mandible; Pre = preanal ring; St = sternite; sub = subanal scale; T = telopodite. Scale bars = 1 mm.

Ostinobolus montanus Wesener, sp. n.

urn:lsid:zoobank.org:act:C67BDE0C-0745-470A-8A2B-01D63253BCC5

Material examined: 6 ♂, 2 ♀ *Holotype:* 1 ♂ (50 mm long), FMMC 8201, Province Toliara, RNI Andohahela, parcel I, 1875 m, 24°33.7' S, 46°43.3' E, camp 5, leg. S. Goodman, 27.XI–5.12.1995. *Paratypes:* 1 ♂, 2 ♀, FMMC 7971, RNI Andohahela, parcel I, camp 4, 1500 m, 24°32.2' S, 46°43.9' E, leg. S. Goodman, 17–27.XI.1995; 1 ♂, FMMC 13610, RNI Andohahela, parcel I, camp 3, 1200 m, 24°35.0' S, 46°44.1' E, leg. S. Goodman, 7–17.XI.1995, pitfall traps.

Other material examined: 3 ♂, CAS BLF 5015 (fm057), RNI Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, montane rainforest, 900 m, 24°45'50" S, 46°45'6" E, leg. B. L. Fisher et al., 21–25.I.2002.

Differential diagnosis: the posterior gonopods of *O. montanus* sp. n. are unique within the Malagasy Spirobolida (Figs 51E, G). For a comparison of *O. stellaris* and *O. montanus*, see above.

Description. *Measurements*: males with 39 or 40 rings, circa 46–52 mm long (broken), 3.8 mm wide. Females (probably immature) with 40 rings, 4.1 mm wide.

Coloration faded in alcohol. Antennae, legs and body rings ventral of ozopore opening reddish (Figs 51A–C). Head greyish (Fig. 51A). Specimens dorsally with a wide, orange stripe flanked by a wide black area extending up to opening of ozopores. *Eyes* with circa 25 ocelli arranged in five rows (Fig. 51A). *Antennae* protruding back to ring 5 (Fig. 51A). *Male coxal processes* only on coxae 3 and 4, short and conical (Fig. 51B). *Preanal process* absent (Fig. 51C).

Anterior gonopod sternite with extraordinarily wide shoulders. Lobe triangular, broadly rounded (Fig. 51D). Sternite tip longer than coxite. Coxite and telopodite inconspicuous, processes absent (Fig. 51F).

Posterior gonopods: basal stem slender and elongated, 5.8 times longer than wide (Fig. 51G). Apical part of telopodite oval (Fig. 51E). Inner margin consisting of a thin membranous area; arm-like projections absent (*x*, *y* in Fig. 51E). Telopodite apically with a large, swollen membranous area. Sperm canal slightly projecting above telopodite margin (Fig. 51G).

Intraspecific variation: too few specimens are known to evaluate the intraspecific variation. The sexual dimorphism in size seems to be less well-developed than in *O. rufus*.

Distribution and ecology: only known from the Andohahela rainforest north of the Isaka-Ivondro corridor (Fig. 49). Specimens were collected from 900–1850 m.

Etymology: *montanus*, adjective, refers to the montane rainforest where this species was collected.

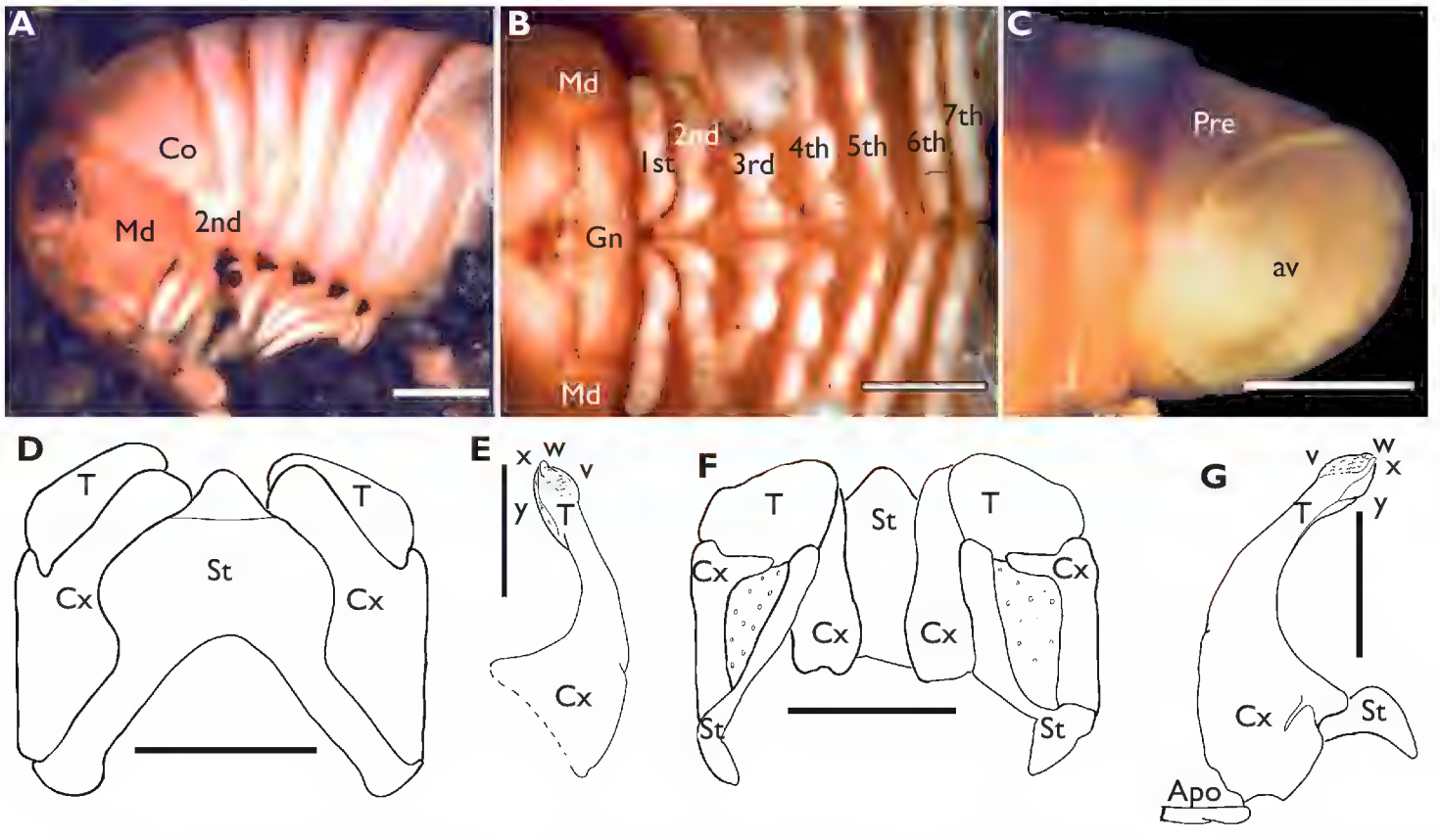

Figure 51. *Ostinobolus montanus* sp. n., male holotype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** anterior gonopod, anterior view **E** right posterior gonopod, anterior view **F** anterior gonopod, posterior view **G** right posterior gonopod, posterior view. av = anal valves Co = collum; Cx = coxite; Gn = gnathochilarium; Md = mandible; Pre = preanal ring; St = sternite; T = telopodite. Scale bars = 1 mm.

***Ostinobolus subterraneus* Wesener, sp. n.**
urn:lsid:zoobank.org:act:F5D60255-4786-4DB3-BA0E-DC3A49AF18EA

Material examined: 2 ♂, 10 ♀, 21 imm. *Holotype:* 1 ♂ (30 mm long), FMMC 8215, Province Toliara, Petriky, 10 m, littoral subhumid forest on sandy soil; 25°3.73' S, 46°52.16' E, leg. B. L. Fisher, Winkler extraction, 22.IX.1998.

Other material examined: 1 ♂, 5 ♀, 8 imm., FMMC W010B, Ambatotsirongorongo Mountain, Forêt Petit Lavasoa, rainforest, 25°05.021' S, 46°46.110' E, leg. T. Wesener et al., 21.V.2007; 1 ♀, ZMH W010B, same data as previous; 4 ♀, 8 imm., W010B, same data as previous, voucher specimens deposited at the University Antananarivo; 3 imm., FMMC W099, Ambatotsirongorongo Mountain, Grand Lavasoa, rainforest, 25°5'10.23" S, 46°44'55.93" E, leg. Wesener et al., 14.VI.2007.

Differential diagnosis: until now, no other species of Spirobolida with a reduced number of ocelli is known from Madagascar. Because of the unusual morphological adaptation to the special life style, the placement of *O. subterraneus* inside *Ostinobolus* is only tentative and less certain than in other Spirobolida species.

Description. *Measurements*: males with 42–44 body rings, circa 30 mm long (broken), 2.7–3.2 mm wide. Females of similar length and width.

Coloration faded in alcohol. Head, legs anal valves, median part of collum and posterior part of metazonites brownish-red. Mesozonites and anterior part of metazonites dark grey (Figs 52A–C). *Eyes* reduced, with circa eight decolorized ocelli (Fig. 52A). *Antennae* protruding back to ring 3 (Fig. 52A). First leg pair elongated, larger than second pair (Fig. 52A). Legs very short, length only 0.4 times body diameter (Fig. 52B). *Male coxal processes* absent (Fig. 52B). *Preanal process* absent, but anal valves not elongated posteriorly like in congeneric species (Fig. 52C).

Anterior gonopod sternite wide. Lobe short, triangular with a sharp tip (Fig. 52E). Sternite tip protruding as high as coxite. Telopodite large, with a well-developed and well-rounded retrorse process, starting at midpoint of telopodite, retrorse part extending beyond telopodite but not coxite (Fig. 52G).

Posterior gonopods: short and wide (Fig. 52F). Apical half of mesal margin filled by a swollen, membranous area. No trace of star-shaped membranous folds. Sperm canal protruding above telopodite margin mesally into a two-tipped lobe (Fig. 52H).

Distribution and ecology: only known from a small area in the extreme southeast of Madagascar. The species is obviously microendemic to the subhumid forest of Petriky and five kilometers south of the isolated rainforest sites on the Ambatotsirongorongo Mountain (Fig. 49). Unlike cave dwelling millipede species, *Ostinobolus subterraneus* sp. n. does not display elongated legs and antennae. The reduced number of ocelli and the elongation of the first leg pair are probably an adaptation to life inside the thick root horizon, the only place where this species was collected.

Etymology: *subterraneus*, adjective, refers to the life deep inside the soil to which this species is adapted.

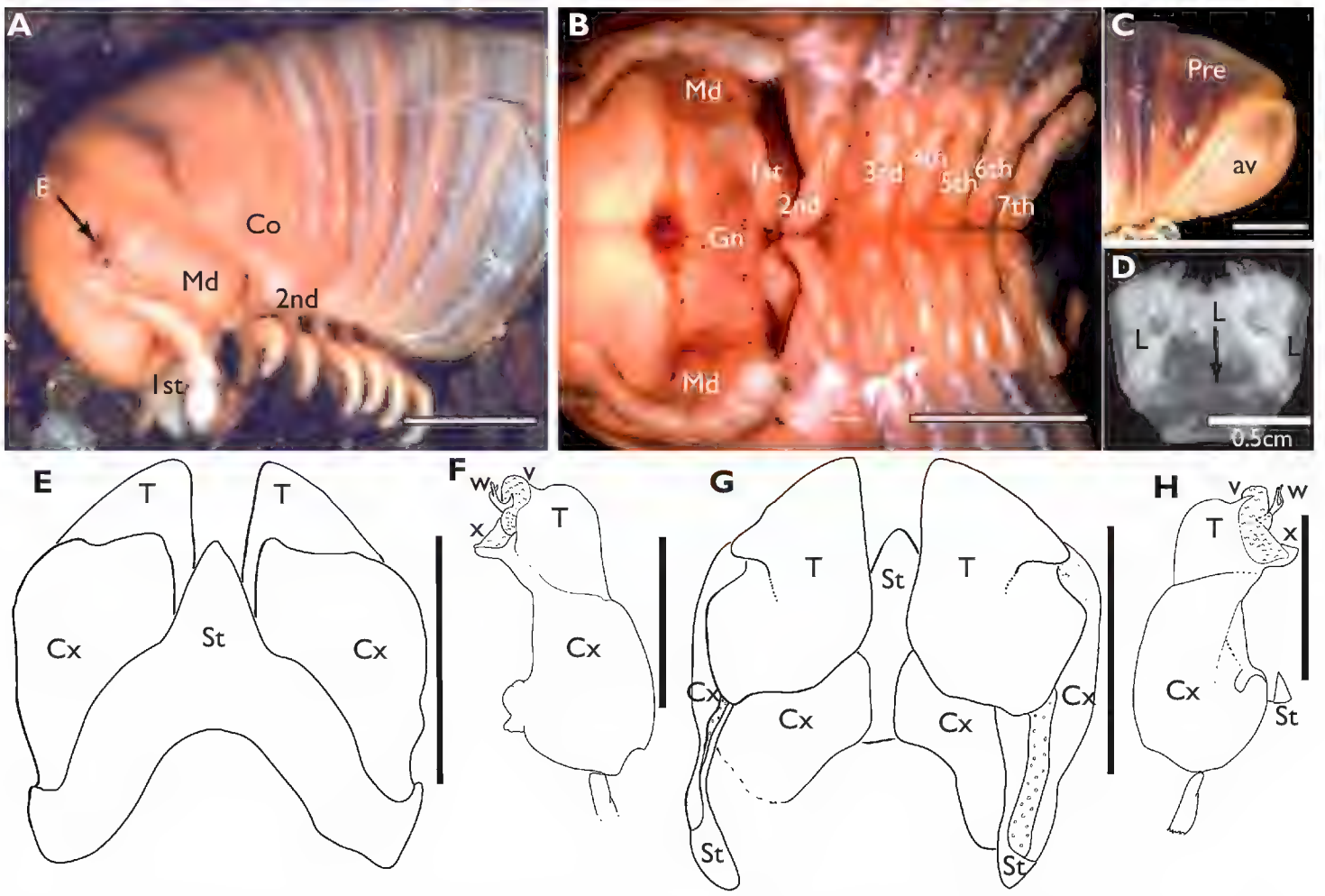

Figure 52. *Ostinobolus subterraneus* sp. n., male holotype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** gnathochilarium, ventral view **E** anterior gonopod, anterior view **F** right posterior gonopod, anterior view **G** anterior gonopod, posterior view **H** right posterior gonopod, posterior view. av = anal valves; Co = collum; Cx = coxite; E = reduced eye; Gn = gnathochilarium; L = ledge; Md = mandible; Pre = preanal ring; St = sternite; T = telopodite. Scale bars = 1 mm.

Suborder Spirobolidea: Family Spirobolellidae

Of special potential phylogenetic interest are the small species of the South American genus *Atlanticobolus* Hoffman, 1979, the West African genus *Amblybolus* Keeton, 1964, as well as the here described Malagasy genus. In these three genera, the posterior gonopod coxites touch one another while a sclerotized sternite is absent. The gonopod pair is nevertheless connected by a membrane. At least the genus *Hylekobolus* gen. n. with its conspicuously elongated posterior gonopods seems to fit well with the Spirobolellidae.

***Hylekobolus* Wesener, gen. n.**
urn:lsid:zoobank.org:act:A90561DE-4844-47EF-8654-19C38A402BA5

Type species: *Hylekobolus brachiosauroides* sp. n.

Other species included:
H. rufus sp. n.
H. griseus sp. n.
H. albicollaris sp. n.
H. goodmani sp. n.
H. montanus sp. n.
H. analavelona sp. n.
H. latifrons sp. n.
H. andasibensis sp. n.
H. marojejy sp. n.
H. anjanaharibe sp. n.

Diagnosis: legs without coxal processes, but coxa 7 in males always twice as wide as coxa 6 (Fig. 55B), a unique feature for Spirobolellidae. The anterior (Figs 55L, N) and posterior gonopods (Figs 55M, O) of *Hylekobolus* are unique within the order Spirobolida. Coxite of posterior gonopods basally at mesal margin with a triangular sclerite (Figs 55O, 56G, 57H, 58G), a potential apomorphy of *Hylekobolus*. Species medium-sized (30 mm) to quite large (75 mm) for species of the Spirobolellidae. Anterior part of body rings usually black, dark grey or reddish, posterior third light brown to white (Figs 53A–C). Telson with a well-rounded preanal process (Figs 55C, 56C), which is however much shorter than in *Granitobolus* or *Pseudocentrobolus* species. Anal valves small, lips absent (Figs 55C, 56C, 57E, 58C, 59C, 60C). Collum ventrally not protruding as far as body ring 2, but anteriorly covering first mandibular basal joint as well as part of antenna (Figs 55A, D). Part of head projecting slightly above second mandibular basal joint (Fig. 55D). Such a modified head capsule (Figs 55D, 57C) and collum (Fig. 55A) are similar to the conditions observed in the South American genus *Atlanticobolus* (Hoffman 1979), as well as the West African genus *Amblybolus* (Keeton 1964), whose family positions are currently unclear (Hoffman 1980). However, in *Hylekobolus* only the second mandibular joint and the collum form a shallow cavity for the short antenna (Fig. 56A), while in *Amblybolus* the area around the ocelli is strongly modified, too (Keeton 1964; Demange and Mauriès 1975). Similar modifications of the head capsule also appear in numerous species of the family Spirobolellidae, for example in the genus *Benoitolus* from the Seychelles Islands (Mauriès 1980). Male legs with tarsal pads only on legs 3–7 (Fig. 55B). Short and wide tarsus with a single pair of long median setae in legs 8 and beyond (Figs 55H, I), unique for Malagasy millipedes. Body ring 7 in males greatly enlarged, ventrally as wide as two regular body rings (Fig. 57B), a character shared only with the Malagasy genus *Spiromimus*. Anterior gonopods prominently elongated (Figs 57E, 58D), especially telopodites (Fig. 55N), tips of anterior gonopods well

Figure 53. Living specimens of **A** *Hylekobolus brachiosauroides* **sp. n.**, male **B** *H. griseus* sp. n., mating pair **C** *H. albicollaris* sp. n.

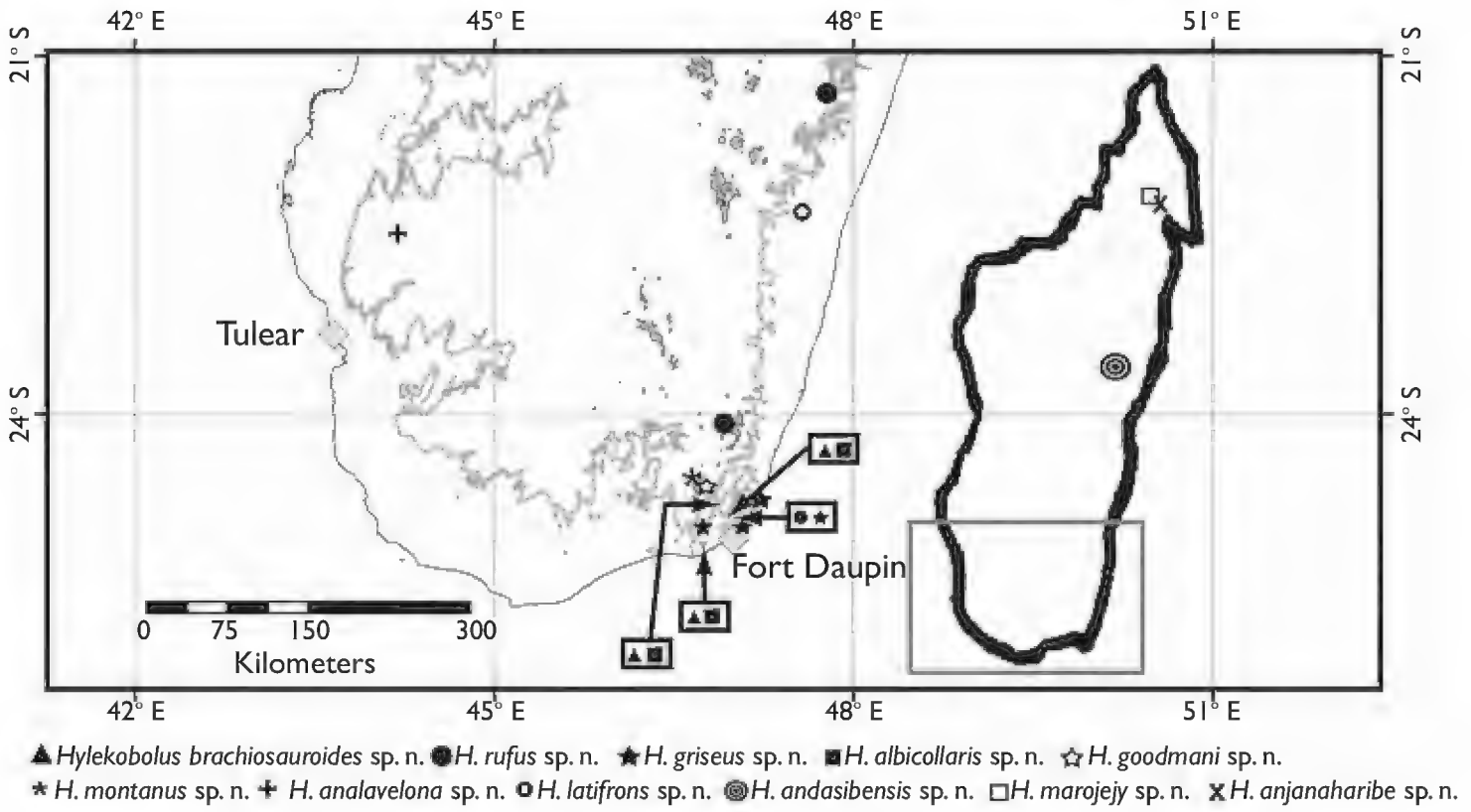
42° E
45° E
48° E
51° E
21° S
24° S
Tulear
Fort Daupin
0 75 150 300
Kilometers
▲ Hylekobolus brachiosauroides sp. n. ● H. rufus sp. n. ★ H. griseus sp. n. ■ H. albicollaris sp. n. ☆ H. goodmani sp. n.
* H. montanus sp. n. + H. analavelona sp. n. ○ H. latifrons sp. n. ◎ H. andasibensis sp. n. □ H. marojejy sp. n. ✕ H. anjanaharibe sp. n.

Figure 54. Distribution map of the genus *Hylekobolus* gen. n.

visible, even in non-dissected specimens (Figs 55B, 57B). Posterior gonopod coxite and telopodite fused, slender and conspicuously elongated (Figs 55O, 56G), which is typical for the species of the family. Telopodites arranged face-to-face with one another. Tip of telopodite bent mesally by 60° (Fig. 34D) or (more often) 90° (Fig. 55O).

Distribution and ecology: all species of *Hylekobolus* were collected in rainforest. Most of the species (6 of 11) were found in Southeastern Madagascar (Fig. 54). This could represent a collection artefact since a larger amount of inventory work was conducted around Tolagnaro (Fort Dauphin). That only few species of *Hylekobolus* occur north of Andasibe is puzzling, as it can hardly be accounted for by the lack of more exhaustive inventories. Of special interest is the occurrence of *Hylekobolus analavelona* sp. n. in the isolated western rainforest of Analavelona. The Analavelona rainforest is isolated by large areas of dry and spiny forest (in which no *Hylekobolus* species was recorded yet) from other humid forests (Moat and Smith 2007). Numerous *Hylekobolus* species are obviously limited in their distribution areas, which have very sharp boundaries (Fig. 54). The mechanisms explaining those boundaries are as little understood as in other Malagasy millipedes.

Large numbers of *Hylekobolus* specimens were found inside dead wood. Single specimens walking on the forest floor were rarely discovered. Two *Hylekobolus* species were often sympatric (Fig. 54). In such instances, one species was always significantly larger than the other (like *H. rufus* sp. n. and *H. albicollaris* sp. n. in Ivorona).

Description. *Size of males and females*: species-specific, species with 42–51 rings, no apodous ring.

Colour highly species-specific, but posterior margin of body rings always of lighter.

Head: each eye with circa 32–48 ocelli arranged in seven vertical rows (Figs 55A, 56A, 57D, 58A). Labrum with standard three irregular teeth and one row of 10–12 stout marginal setae. Clypeus with two setiferous foveolae on each side (Figs 57B, D). Head around incisura lateralis projecting slightly above basal joints of mandible (Figs 55D, 57C). Head projection and basal mandible joint forming antennal cavity. Antennae short, protruding back to body ring 2 (Figs 55A, 56A, 57A). Relative lengths of antennomeres: 1<<2>3=4=5<6 (Figs 55A, 61A). Terminal antennomere with four large sensory cones located together inside a membranous area (Fig. 61A). Antennomere 5 latero-apically with four rows (Fig. 61B), antennomere 6 with two rows (Fig. 61C) of sensilla basiconica.

Gnathochilarium lamellae linguales each with two standard setae located behind one another (Fig. 55E). Stipites each with three apical setae. Mentum not subdivided, basally with several sclerotized ridges (Figs 55E, F). Stipites towards mentum with circa three weakly-developed, sclerotized ledges (Fig. 55G). Hypopharyngeal crest with a field of spine-like structures (Fig. 61D). Central pads of endochilarium separated into two areas, apically with circa eight, basally with >20 sensory cones (Fig. 61D).

Mandible: external tooth simple, rounded; mesal tooth with three well-developed cusps and in some species with an additional fourth, shallow cusp (Fig. 61E). Basal most cusp extraordinarily large and sharp-edged (Fig. 61E). Four or five pectinate lamellae. Molar plate towards pectinate lamellae with a large furrow and circa eight smaller posterior furrows (Fig. 61E).

Collum: smooth, ventrally not protruding as far as ring 2 (Fig. 57B). Collum covering basal mandibular joint anteriorly (Fig. 55A), as well as part of antenna (Fig. 56A).

Body rings: dorsally and laterally with micropunctation, meso- and metazona ventrally with numerous transverse impressions. Ozopores starting at ring 6, touching suture between mesozona and metazona (Fig. 55A).

Telson: preanal process protruding, well-rounded, slightly curved ventrally (Figs 55C, 56C, 57E, 58C). Anal valves short, smooth, with neither grooves, nor lips, nor micropunctation (Fig. 55C). Subanal scale inconspicuous (Fig. 55C).

Legs: coxae 1 and 2 elongated and fused with sternum, podomeres from prefemur to tarsus in both sexes each with 4–10 ventral/mesal setae. Length of midbody legs in males 0.6–0.7 (Fig. 55H), in females 0.4–0.5 times body diameter (Fig. 55I). Each podomere with a long, apical, ventral seta. Coxae 3 and beyond of rectangular shape (Fig. 55H). Tarsus with a tiny dorso-apical seta and a pair of extraordinary long ventral setae (Figs 55H, I).

Male sexual characters: tarsal pads present only on legs 3–7 (Figs 55B, 60A). Coxae 3–7 without processes, but coxa 7 twice as wide as coxa 6 (Figs 55B, 56B, 57B). Ring 7 large, in ventral view twice as wide as normal rings (Figs 55B, 57B).

Anterior gonopods: prominently elongated, tips projecting from gonopod pouch (Figs 55B, 57B). Anterior gonopods basally with a small sternal apodeme (Fig. 55L), coxite and telopodite apodeme absent. Sternite always well-developed, but hyaline (sheer), of species-specific shape, either triangular (Fig. 55L), rectangular (Fig. 56D), or well-rounded (Fig. 60D). Coxites wide, in some species mesally with a wide, well-rounded process (Figs 57E, 58D, 59D). Telopodites large, elongated (Fig. 55N), mesally protruding into a wide, well-rounded process (Figs 55N, 56F). Mesal margins of process often large and widely protruding (Figs 56F, 58F). Margins basally of process in some species additionally protruding (Fig. 57G).

Posterior gonopods resembling long neck and small head of dinosaurs belonging to the Sauropoda group (Figs 55M, O). Coxite and telopodite fused, a suture partially visible (Fig. 55O). Sternite absent (Figs 55O, 56G), posterior gonopods nevertheless connected via membranes. Coxite conspicuously elongated (Figs 55O, 56G, 57F, H), basally at mesal margin with a triangular sclerite, median part of sclerite membranous (Figs 55O, 56G). Coxite mesally with a single spermatic groove. Telopodites arranged face-to-face with one another, tips bent mesally by 60° (Fig. 64D) or (more often) 90° (Fig. 55O). Apically at lateral margin often with a well-rounded short projection (*w* in Figs 55M, 56E). Sperm canal apically protruding above telopodite margin (*z* in Figs 55M, 56E). Telopodite often with an apical process protruding as continuance of tip (*x* in Figs 55M, 56E). A single membranous lobe (*y*) often present between (*x*) and (*z*) (Figs 55M, 56E), lobe in one species greatly enlarged (Fig. 66B). Apodeme very long, oriented in 90° angle towards gonopod (Figs 55O, 56G, 59G).

Female sexual characters: vulva simple, bivalve-like (Fig. 55J), with a small, poorly sclerotized operculum at base (Fig. 55K). Posterior valve apically slightly overlapping anterior one (Fig. 61F). Both valves smooth, sensory cones absent. Two or three rows of setae basally on each valve (Fig. 61F).

Etymology: *Hylekobolus*, Latin, masculine, consisting of "hyleko", short form of *hylekoites* Greek, m., dweller in wood, which refers to the ecology of this species, and *-bolus*.

Key to the *Hylekobolus* species:

1 Telopodite of posterior gonopod apically with a greatly enlarged membranous area (*y* in Fig. 66B). Whole posterior gonopod unusually wide ..... ***H. anjanaharibe* sp. n.**

– Telopodite of posterior gonopod, membranous area (*y*) not greatly enlarged. Posterior gonopod very slender (Fig. 55O) **2**

2 Apical process of anterior gonopod telopodite tapering towards tip, laterally not projecting (Fig. 34C). Telopodite of posterior gonopod not bending 90° but only 60° (Fig. 64D) ..... ***H. andasibensis* sp. n.**

– Apical process of anterior gonopod telopodite laterally always with a well-rounded, wide projection (Fig. 55N). Telopodite of posterior gonopod always bending 90° (Fig. 55O) **3**

3 Apical process (*x*) of posterior gonopod enlarged and triangular. Sperm canal discharging on tip (Figs 65B, D) ..... ***H. marojejy* sp. n.**

– Apical process (*x*) of posterior gonopod never triangular (Fig. 55O). Sperm canal on special branch (z) protruding above gonopod **4**

4 Apical process (*x*) of posterior gonopod wide and membranous (Figs 57F, 58E). Sternite of anterior gonopod slender, triangular (Figs 57E, 58D) **5**

– Apical process (*x*) of posterior gonopod always completely sclerotized (Fig. 55M). Sternite of anterior gonopod rectangular (Fig. 56D), if triangular then not slender (Fig. 55L) **6**

5 Central part of collum and anterior half of telson dark grey (Figs 53B, 57A). Retrorse process of anterior gonopod laterally not protruding above telopodite margin (Fig. 57G). Telopodite of posterior gonopod without a membranous lobe (Figs 57F, H) ..... ***H. griseus* sp. n.**

– Collum and telson shiny white (Figs 53C, 58A). Retrorse process of anterior gonopods laterally slightly protruding above telopodite margin (Fig. 58F). Telopodite of posterior gonopod with a membranous lobe (*y* in Figs 58E, G) ..... ***H. albicollaris* sp. n.**

6 Lateral margin (*w*) of posterior gonopod apically with a thick, swollen, well-rounded projection (Figs 55M, 60E). Apical process (*x*) basally wide, apically extended into a slender projection (Fig. 55M) 7

– Lateral margin of posterior gonopod without a swollen projection (Figs 56E, 59E, *w*). Apical process (*x*) either wide (Fig. 56E) or slender (Fig. 59E) **8**

7 Collum in anterior half entirely red or white (Figs 53A, 55A). Sternite of anterior gonopods wide, triangular (Fig. 55L). Retrorse process of anterior gonopod laterally not protruding above telopodite (Fig. 55N). Apical process (*x*) of posterior gonopod basally with a protruding margin (Fig. 55M) ..... ***H. brachiosauroides* sp. n.**

– Collum grey, only at margins white (Fig. 60A). Sternite of anterior gonopods wide and well-rounded (Fig. 60D). Retrorse process of anterior gonopod laterally widely protruding above telopodite (Fig. 60F). Apical process (*x*) of

posterior gonopod basally wide, but not protruding (Fig. 60E) ..... ***H. montanus* sp. n.**

8 Apical process (*x*) of posterior gonopod wide (Figs 56E, 63B). Retrorse process of anterior gonopod slightly protruding above telopodite lateral margin (Fig. 56F)..... **9**

– Apical process (*x*) of posterior gonopod slender (Fig. 59E). Retrorse process of anterior gonopod widely protruding above telopodite lateral margin (Fig. 59F) **10**

9 Collum entirely red (Fig. 56A). Sternite of anterior gonopod wide and rectangular (Fig. 56D). Telopodite of posterior gonopod slender, 4 times longer than wide (Fig. 56G). Males 60–65 mm long, 4.8–4.9 mm wide with 49–52 rings..... ***H. rufus* sp. n.**

– Collum anteriorly light, posteriorly darker grey. Sternite of anterior gonopod triangular (Fig. 63A). Telopodite of posterior gonopod very wide, 2 times longer than wide (Fig. 63D). Male 47 mm long, 4.2 mm wide with 46 or 47 rings..... ***H. latifrons* sp. n.**

10 Central part of collum and anterior 3/4 of body rings dark grey (Fig. 59A). Mesal coxite process of anterior gonopod well-developed (Fig. 59D). Retrorse telopodite process relatively slender, but widely projecting (Fig. 59F). Apical process (*x*) of posterior gonopod almost as slender as projection of sperm canal (Fig. 59E) ..... ***H. goodmani* sp. n.**

– Collum and posterior half of body rings light brown (Fig. 62A). Body rings in anterior half only laterally with dark green colour, dorsally light brown. Each body ring dorsally with an isolated dark green spot. Mesal coxite process of anterior gonopod short (Fig. 62D). Retrorse telopodite process wide and projecting (Fig. 62F). Apical process (*x*) of posterior gonopod 4–5 times as wide as sperm canal (Fig. 62E) ..... ***H. analavelona* sp. n.**

***Hylekobolus brachiosauroides* Wesener, sp. n.**
urn:lsid:zoobank.org:act:40FD10B2-63FB-4627-AAAC-6961BE9102E5

Material examined: 26 ♂, 21 ♀, 6 imm. *Holotype:* 1 ♂ (55 mm long), FMMC W089, Vohimena Mountains, West slope, Ivorona, 114 m, rainforest, 24°50.026' S, 46°56.943' E, leg. Wesener et al., 23.V.2007. *Paratypes:* 3 ♂, 4 ♀, FMMC W089, same data as holotype; 1 ♂, 1 ♀, ZMUC W089, same data as holotype; 1 ♂, ZMH W089, same data as holotype; 1 ♂, 1 ♀, CAS W089, same data as holotype; 1 ♂, ZSM W089, same data as holotype.

Other material examined: 4 ♂, 4 ♀, W089, same data as holotype, voucher specimens deposited at the University Antananarivo; 5 ♂, 4 ♀, 2 imm., FMMC W049B, Andohahela, Isaka-Ivondro Sud, 46 m, rainforest, 24°49.690' S, 46°51.971' E, leg. Wesener et al., 08.VI.2007; 5 ♂, 4 ♀, 2 imm., W049B, same data as previous, voucher specimens deposited at the University Antananarivo; 2 ♂, 2 ♀, FMMC W099, Ambatotsirongorongo Mountain, Grand Lavasoa, rainforest, 25°5'10.23" S, 46°44'55.93"

E, rainforest, leg. Wesener et al., 14.VI.2007; 2 ♂, 1 ♀, 2 imm., W099, same data as previous, voucher specimens deposited at the University Antananarivo.

Differential diagnosis: *H. brachiosauroides* differs in size and colour from the sympatric living *H. albicollaris* sp. n. The posterior gonopods (Figs 55M, O) of *H. brachiosauroides* differ from other, same-sized *Hylekobolus* species: the lateral margin carries a thick, swollen, well-rounded projection (Fig. 55M), a feature only shared with *H. montanus* sp. n. *H. brachiosauroides* differs from *H. montanus* sp. n. in the presence of a protruding apical process (*x*) on the posterior gonopods, a weakly protruding lateral retrorse process of the anterior gonopod (Fig. 55N), and a different colour pattern.

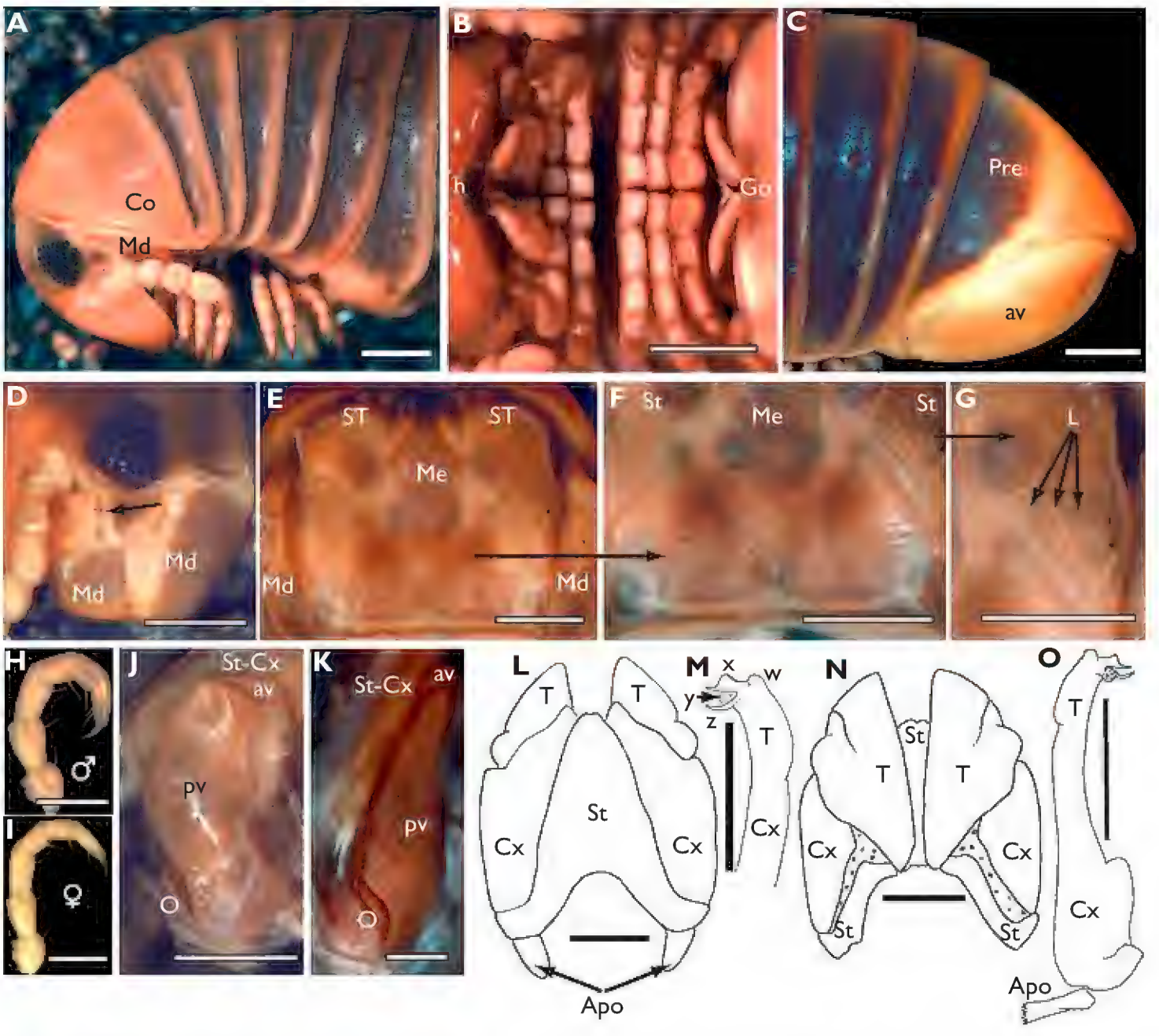

Figure 55. *Hylekobolus brachiosauroides* sp. n., A–H male paratype, I–K female paratype, L–O male holotype. **A** head, lateral view **B** legs 1–7 and gonopods, ventral view **C** telson **D** antennal groove **E** gnathochilarium, ventral view **F** gnathochilarium, mentum **G** gnathochilarium, stipites **H, I** right midbody legs **J** right vulva, posterior view **K** right vulva, lateral view **L** anterior gonopod, anterior view **M** right posterior gonopod, anterior view **N** anterior gonopod, posterior view **O** right posterior gonopod, posterior view. Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; Go = gonopods; h = head; IL = incisura lateralis; L = ledges; Md = mandible; Me = mentum; O = operculum; Pre = preanal ring; pv = posterior valve; St = sternite; St-Cx = sterno-coxite; ST = stipites; T = telopodite. Scale bars = 1 mm.

Description. *Measurements*: males with 50 or 51 rings, 53–62 mm long, 4.8–5.2 mm wide. Females with 50 or 51 rings, 58–72 mm long, 5.1–6.0 mm wide.

Coloration: anterior part of head and collum, posterior part of telson and posterior margin of body rings lightly red or white (Figs 53A, 55A, C). Legs and antennae white (Fig. 53A). Anterior part of body rings, telson, posterior part of head and collum black (Figs 53A, 55A). *Eyes* with 40–44 ocelli (Fig. 55D).

Anterior gonopod sternite basally wide, apically elevated into a triangular lobe with a triangular, wide, well-rounded tip (Fig. 55L). Mesal process of coxite wide and only slightly protruding (Fig. 55L). Apical process of telopodite large and well-rounded. Retrorse margin wide, not projecting above telopodite margin (Fig. 55N). Margin of apical process basally wide and projecting (Fig. 55N).

Posterior gonopods telopodite bent 90° (Fig. 55O). Lateral margin with a thick, swollen, well-rounded projection (*w*, Fig. 55M). Apical process (*x*) apically slender, basally with a widely protruding margin (Fig. 55M). Membranous lobe (*y*) rectangular (Fig. 55M). Projection of sperm canal (*z*) long and slender, slightly curved towards apical process (Fig. 55M).

Intraspecific variation: coloration of the posterior margin of body ring varies in adults between white and reddish, while it is always white in imm..

Distribution and ecology: this species was found in the isolated Ambatotsirongorongo Mountain, the Andohahela Isaka-Ivondro corridor as well as on the western slopes of the Vohimena Mountain (Fig. 54). *H. brachiosauroides* could not be collected north of the Isaka-Ivondro corridor, where *H. goodmani* sp. n. and *H. montanus* sp. n. occur. In the eastern Vohimena slopes, *H. rufus* sp. n. replaces *H. brachiosauroides*. All individuals were collected inside dead logs.

Etymology: *brachiosauroides*, adjective, refers to the dinosaur genus *Brachiosaurus*, whose neck and head closely resemble the general shape of the posterior gonopods of this millipede.

Hylekobolus rufus Wesener, sp. n.

urn:lsid:zoobank.org:act:DA4510C8-7395-4FC6-B2E5-4FD125250FB4

Material examined: 14 ♂, 8 ♀, 1 imm. *Holotype:* 1 ♂ (60 mm long), FMMC 8188, Province Fianarantsoa, PN Midongy, Mt. Papango, 3.5 km SW Befotaka, rainforest, 1250 m, 23°50.3' S, 46°57.5' E, leg. S. Goodman, 2–7.XI.1997. *Paratype:* 1 ♀, FMMC 8188, same data as holotype; 1 ♂, 1 imm., FMMC 6172, Province Fianarantsoa, PN Midongy, Mt. Papango, 2.5 km SW Befotaka, rainforest, 875 m, 23°50.1'S, 46°57.8'E, leg. S. Goodman, 26–31.X.2003, pitfall trap.

Other material examined: 2 ♂, 1 ♀, FMMC W092, Province Toliara, Vohimena Eastern Slope, Enato, rainforest, 24°53'0.25" S, 46°59'2.77" E, leg. T. Wesener et al., 27.V.2007; 2 ♂, MNHN, Province Fianarantsoa, Tolongoina, route d'Ifanadiana, Fort Carnot, 21°33' S, 47°31' E, Rec. Blanc, 18.V.1964; 1 ♂, MNHN, Province Fianarantsoa, Befotaka (p. de Farafangana), 600 m, Région montagneuse boisée, 23°49' S, 46°59' E, leg. entrée 17–1927, R. Decary, 10.VIII.1926; 7 ♂, 6 ♀, CAS NoNumber,

Province Fianarantsoa, PN Ranomafana, Talatakely, 21°14.9' S, 47°25.6' E, leg. C. Griswold et al., 19–30.IV.1998.

Differential diagnosis: *H. rufus* differs from all other *Hylekobolus* species in a unique combination of characters: collum red (Fig. 56A), posterior gonopod at lateral margin (*w*) lacking projection, apical process (*x*) wide (Fig. 56E).

Description. *Measurements*: males with 50–52 rings, 55–65 mm long, 4.1–4.8 mm wide. Females with 50 or 51 rings, circa 63 mm long, 5.7 mm wide.

Coloration in numerous samples affected by alcohol. Head, collum, antennae, legs, metazonites of body rings and posterior part of telson including anal valves and subanal scale red (Figs 56A, C). Anterior part of body rings and telson dark grey (Figs 56A, C). *Eyes* with 32–34 ocelli (Fig. 56A).

Anterior gonopod sternite basally wide, completely rectangular, apically even slightly wider than basally (Fig. 56D). Mesal process of coxite wide and only slightly protruding (Fig. 56D). Apical process of telopodite large and well-rounded. Retrorse margin wide, projecting above telopodite margin (Fig. 56F) but not protruding basally of apical process (Fig. 56F).

Posterior gonopods telopodite bent 90° (Fig. 56G). Lateral margin without a projection (*w*, Fig. 56E). Apical process (*x*) wide (Fig. 56E). Membranous lobe (*y*) large and

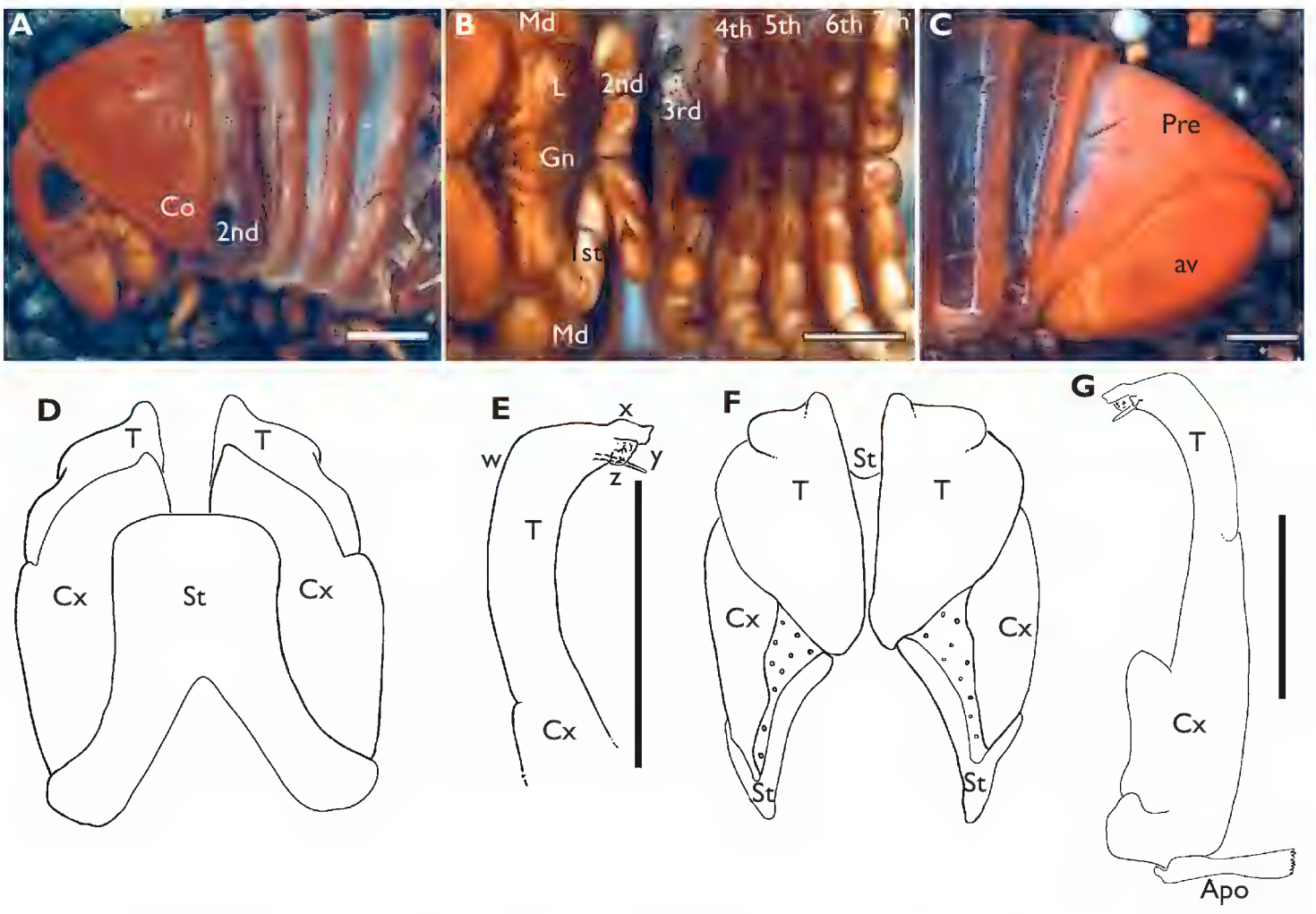

Figure 56. *Hylekobolus rufus* sp. n., male holotype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** anterior gonopod, anterior view **E** left posterior gonopod, anterior view **F** anterior gonopod, posterior view **G** left posterior gonopod, posterior view. Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; Gn = gnathochilarium; L = ledges; Md = mandible; Pre = preanal ring; St = sternite; T = telopodite. Scale bars = 1 mm.

rectangular (Fig. 56E). In posterior view, an additional small, sclerotized lobe present apically of membranous lobe (Fig. 56G). Projection of sperm canal (*z*) straight, as long as apical process (Fig. 56G).

Distribution and ecology: *H. rufus* is the *Hylekobolus* species with the largest area of distribution. It occurs in Southeastern Madagascar from the eastern slopes of the Vohimena range, Midousy Mountains up to Tolongoina (Fig. 54).

Etymology: *rufus*, adjective, refers to the reddish colour pattern (Fig. 56A).

Hylekobolus griseus Wesener, sp. n.

urn:lsid:zoobank.org:act:7BCC2A1D-F354-4402-8E85-53BF01FCD0A7

Material examined: 24 ♂, 32 ♀, 37 imm. *Holotype:* 1 ♂ (40 mm long), FMMC W092A, Vohimena Eastern Slope, Enato, rainforest, 24°53'0.25" S, 46°59'2.77" E, leg. T. Wesener et al., 27.V.2007 *Paratypes:* 5 ♂, 5 ♀, 6 imm., FMMC W092A, same data as holotype; 1 ♂, 1 ♀, ZMUC W092A, same data as holotype; 1 ♂, 1 ♀, ZMH W092A, same data as holotype; 1 ♂, 1 ♀, CAS W092A, same data as holotype; 1 ♂, 1 ♀ ZSM W092A, same data as holotype.

Other material examined: 5 ♂, 6 ♀, 6 imm., W092A, same data as holotype, University Antananarivo; 1 ♂, FMMC, Province Toliara, Sainte Luce, S9, littoral forest on sand, 24°47'S, 47°10'E, leg. T. Wesener, 06.IV.2003; 2 ♂, 2 ♀, 6 imm., FMMC W029, Sainte Luce, S9, littoral forest on sand, 12 m, 24°46.769' S, 47°10.288' E, leg. T. Wesener et al., 01.VI.2007; 1 ♂, 3 ♀, 6 imm., W029, same data as previous, University Antananarivo; 2 ♂, 5 ♀, 2 imm. FMMC W038, Mandena, littoral forest on sand, 34 m, 24°57.260' S, 46°59.499' E, leg. T. Wesener et al., 02.VI.2007; 2 ♂, 5 ♀, 3 imm., W038, same data as previous, University Antananarivo; 1 ♂, 1 ♀, 4 imm., FMMC W044B, Andohahela, Malio, rainforest, 24°55.810' S, 46°46.343' E, leg. T. Wesener et al., 30.V.2007; 1 ♀, 4 imm., W044B, same data as previous, University Antananarivo.

Differential diagnosis: *H. griseus* can only be confused with *H. albicollaris* sp. n., which shares the small body size and a wide and partly membranous apical process (*x*) on the posterior gonopods (Fig. 57G). Both species differ in colour pattern (compare Fig. 57A with Fig. 58A) and also slightly in the gonopod structure.

Description. *Measurements*: males with 44–47 rings, 38–45 mm long, 3.5–3.9 mm wide. Females with 44–47 rings, 37–45 mm long, 3.8–4.65 mm wide.

Coloration: collum margins, posterior part of telson and posterior margin of body rings white (Figs 53B, 57A, E). Legs and antennae white (Fig. 53B). Anterior part of body rings, telson, head and collum dark grey (Figs 53B, 57A, E). *Eyes* with 36–40 ocelli (Fig. 57C).

Anterior gonopod sternite basally wide, apically elevated into a slender, triangular lobe with a well-rounded tip (Fig. 57E). Mesal process of coxite slender and protruding (Fig. 57E). Apical telopodite process large and well-rounded. Retrorse margin wide, not projecting above telopodite (Fig. 57G); margin basally of apical process wide, projecting (Fig. 57G).

Posterior gonopods telopodite bent 90° (Fig. 57F). Lateral margin without a projection (*w*, Fig. 57F). Apical process (*x*) wide, swollen and membranous (Fig. 57H). A membranous lobe (*y*) absent (Fig. 57F). Projection of sperm canal (*z*) extraordinary long and slender, widely extending beyond apical process (Fig. 57H).

Distribution and ecology: *H. griseus* sp. n. is widely distributed in the south-eastern part of the littoral rainforest, as well as on the eastern slopes of the Vohimena

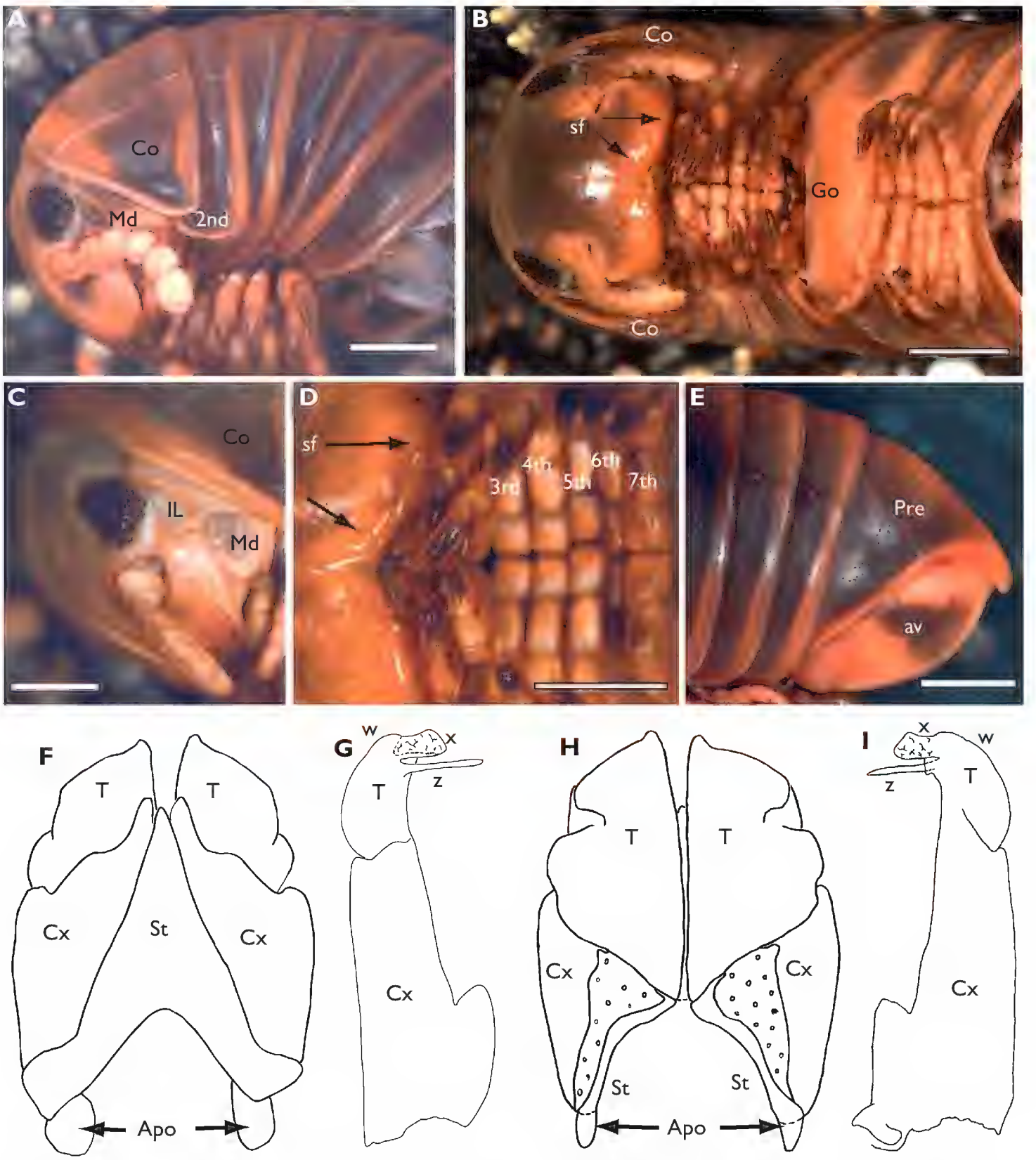

Figure 57. *Hylekobolus griseus* sp. n., A–E male paratype, F–I male holotype. **A** head, lateral view **B** legs 1–7 and gonopods, ventral view **C** antennal groove **D** legs 1–7, ventral view **E** telson **F** anterior gonopod, anterior view **G** left posterior gonopod, anterior view **H** anterior gonopod, posterior view **I** left posterior gonopod, posterior view. Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; Go = gonopods; IL = incisura lateralis; Md = mandible; Pre = preanal ring; sf = setiferous foveolae; St = sternite; T = telopodite. Scale bars = 1 mm.

Mountains. It also occurs in Malio, located on the eastern slopes of the Anosy Mountains. The absence of *H. griseus* from the Ambatotsirongorongo Mountain, which lies in the middle of its range, is enigmatic (Fig. 54). At Ambatotsirongorongo, as well as on the western slopes of the Vohimena Mountains and in the Andohahela Isaka-Ivondro corridor, *H. griseus* is replaced by *H. albicollaris* sp. n. All specimens were collected in dead wood, as well as in mould which assembled in the axis of *Pandanus* leaves.

Etymology: *griseus*, adjective, refers to the dark grey colour of this species.

Hylekobolus albicollaris Wesener, sp. n.

urn:lsid:zoobank.org:act:1E02878D-956E-4FFB-8175-15B8ECB7D5F6

Material examined: 18 ♂, 23 ♀, 18 imm. *Holotype:* 1 ♂ (35 mm long), FMMC W084, Western slope of Vohimena Mountains, Ivorona, rainforest, 114 m, 24°50.026' S, 46°56.943' E, leg. T. Wesener et al., 23.V.2007 *Paratypes:* 1 ♂, 1 ♀, FMMC W084, same data as holotype; 1 ♂, 1 ♀, ZMUC W084, same data as holotype; 1 ♂, ZMH W084, same data as holotype; 1 ♂, 1 ♀, CAS W084, same data as holotype; 1 ♂, ZSM W084, same data as holotype.

Other material examined: 2 ♂, 9 ♀, 3 imm., W089, same data as holotype, University Antananarivo; 1 ♀, FMMC W048D, Andohahela, Isaka-Ivondro Sud, rainforest, 46 m, 24°49.690' S, 46°51.971' E, leg. T. Wesener et al., 08.VI.2007; 5 ♂, 5 ♀, 7 imm., FMMC W008, Ambatotsirongorongo Mountain, Petit Lavasoa, rainforest, 668 m, 25°05.021' S, 46°46.110' E, leg. T. Wesener et al., 21.V.2007; 5 ♂, 5 ♀, 8 imm., **W008**, same data as previous, University Antananarivo.

Differential diagnosis: the colour pattern of *Hylekobolus albicollaris* is unique for Malagasy species of Spirobolida and allows an easy identification in the field. For a separation of *H. albicollaris* and *H. griseus* see above.

Description. *Measurements*: males with 42–45 rings, 33–36 mm long, 2.7–3.1 mm wide. Females with 42–46 rings, 30–36 mm long, 3.0–3.6 mm wide.

Coloration: anterior part of head, entire collum and telson as well as posterior margin of body rings, legs and antennae white (Figs 53C, 58A, C). Posterior part of head and anterior 2/3 of body rings dark grey to black (Figs 53C, 58A). *Eyes* with 32–34 ocelli (Fig. 58A).

Anterior gonopod sternite basally wide, apically elevated into a slender, triangular lobe with a well-rounded tip (Fig. 58D). Mesal coxite process slender and protruding (Fig. 58D). Apical process of telopodite large and well-rounded. Retrorse margin wide, widely projecting above telopodite margin (Fig. 58F); margin basally of apical process not projecting (Fig. 58F).

Posterior gonopods telopodite bent 90° (Fig. 58G). Lateral margin without a projection (*w*, Fig. 58E). Apical process (*x*) wide, swollen and membranous (Fig. 58E). A membranous lobe (*y*) present, in posterior view overlapping part of sperm canal (Fig. 58E). Projection of sperm canal (*z*) extraordinary long and slender, twice as long as apical process (Fig. 58G).

Distribution and ecology: this species was found in the isolated Ambatotsirongorongo Mountain, the Andohahela Isaka-Ivondro corridor as well as on the western slopes of the Vohimena Mountains (Fig. 54). *H .brachiosauroides* occurs sympatrically at all three sites. *H. albicollaris* sp. n. was not found at the Malio sites in the southern Anosy Mountains, the eastern slopes of the Vohimena Mountains or in the lowland littoral rainforests of Mandena and Sainte Luce, where the species is replaced by *H. griseus* sp. n.

Etymology: *albicollaris* refers to the white collum (Fig. 53C) of this species, a unique feature for Malagasy Spirobolida.

Hylekobolus goodmani Wesener, sp. n.

urn:lsid:zoobank.org:act:C097B4BE-0F42-4C7D-B087-4C7B4396C826

Material examined: 6 ♂, 3 ♀ *Holotype:* 1 ♂ (hind end missing), FMMC 7936, Province Toliara, RNI Andohahela parcel I, 440 m, rainforest, 24°37.6' S, 46°45.9' E, leg. S. Goodman, 19–28.X.1995. *Paratypes:* 2 ♂, 1 imm., FMMC 8190, Province Toliara,

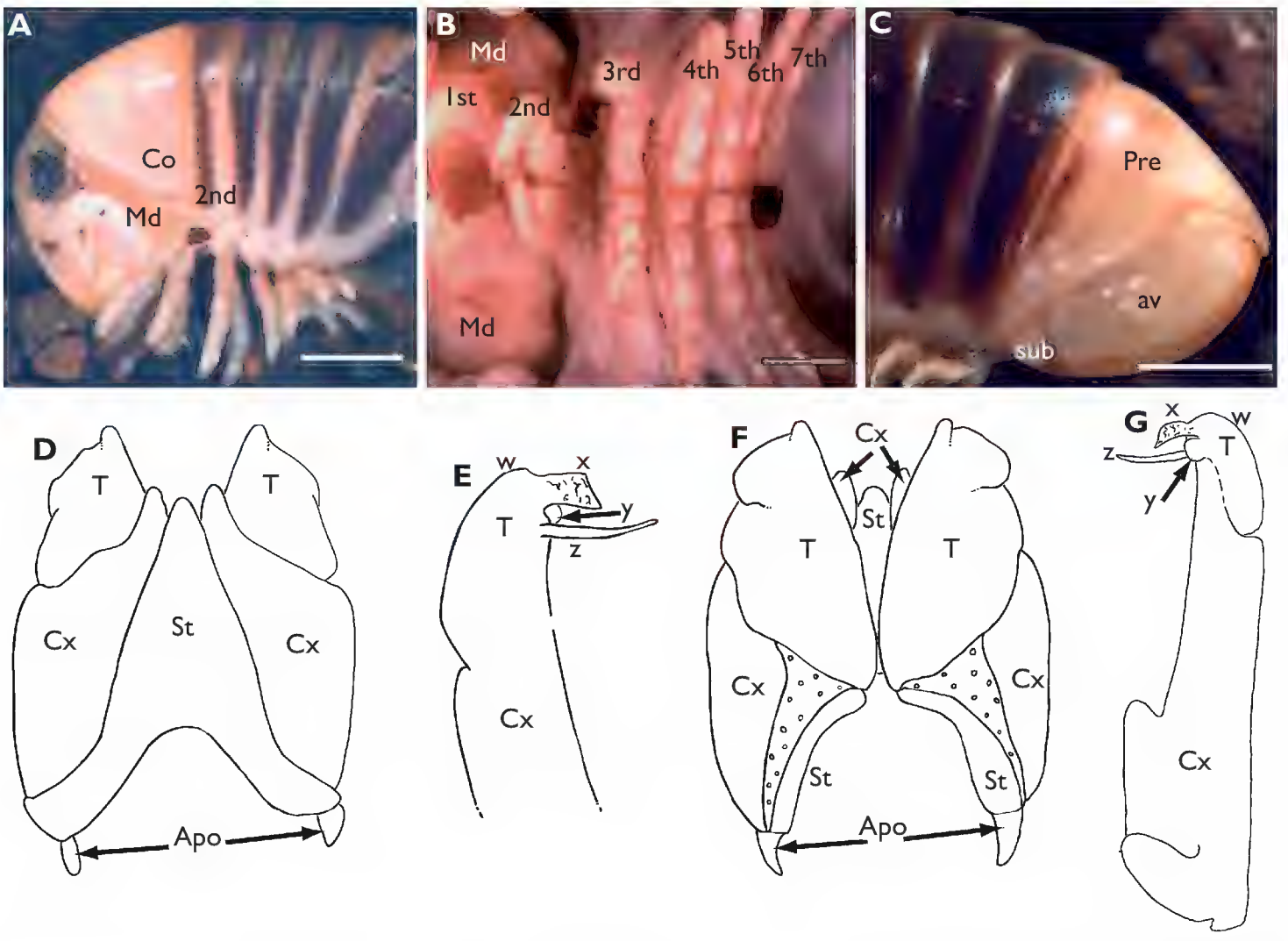

Figure 58. *Hylekobolus albicollaris* sp. n., male holotype. **A** head, lateral view **B** male legs 1–7, ventral view **C** telson **D** anterior gonopod, anterior view **E** left posterior gonopod, anterior view **F** anterior gonopod, posterior view **G** left posterior gonopod, posterior view. Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; Md = mandible; Pre = preanal ring; St = sternite; sub = subanal scale; T = telopodite. Scale bars = 1 mm.

RNI Andohahela parcel I, 1200 m, rainforest, 24°35.0' S, 46°44.1' E, leg. S. Goodman, 7–17.XI.1995;

Other material examined: 2 ♂, 1 ♀, FMMC 8191, same data as previous; 1 ♂, 2 ♀, FMMC 8202, RNI d' Andohahela parcel 1, 1875 m, montane rainforest, 24°33.7' S, 46°43.3' E, pitfall traps, leg. S. Goodman, 5.XII.1995.

Differential diagnosis: the gonopods clearly identify this species (Figs 59D–G). *H. goodmani* is quite similar in colour to the sympatric *H. montanus* sp. n. The latter, however, is much larger and has completely different posterior gonopods.

Description. *Measurements*: male holotype with 49 rings, 55 mm long, 4.7–4.9 mm wide.

Coloration: head, median part of collum, anterior 3/4 of body rings and anterior half of anal segment dark grey (Fig. 59A). Posterior margin of body rings, telson and margins of collum light brown (Fig. 59C). Legs light brown, antennae darker grey (Fig. 59B). *Eyes* with 40–44 ocelli (Fig. 59A).

Anterior gonopod sternite basally wide, apically elevated into a rectangular lobe with a well-rounded tip (Fig. 59D). Mesal process of coxite slender and protruding (Fig. 59D). Apical process of telopodite large and well-rounded. Retrorse margin slender,

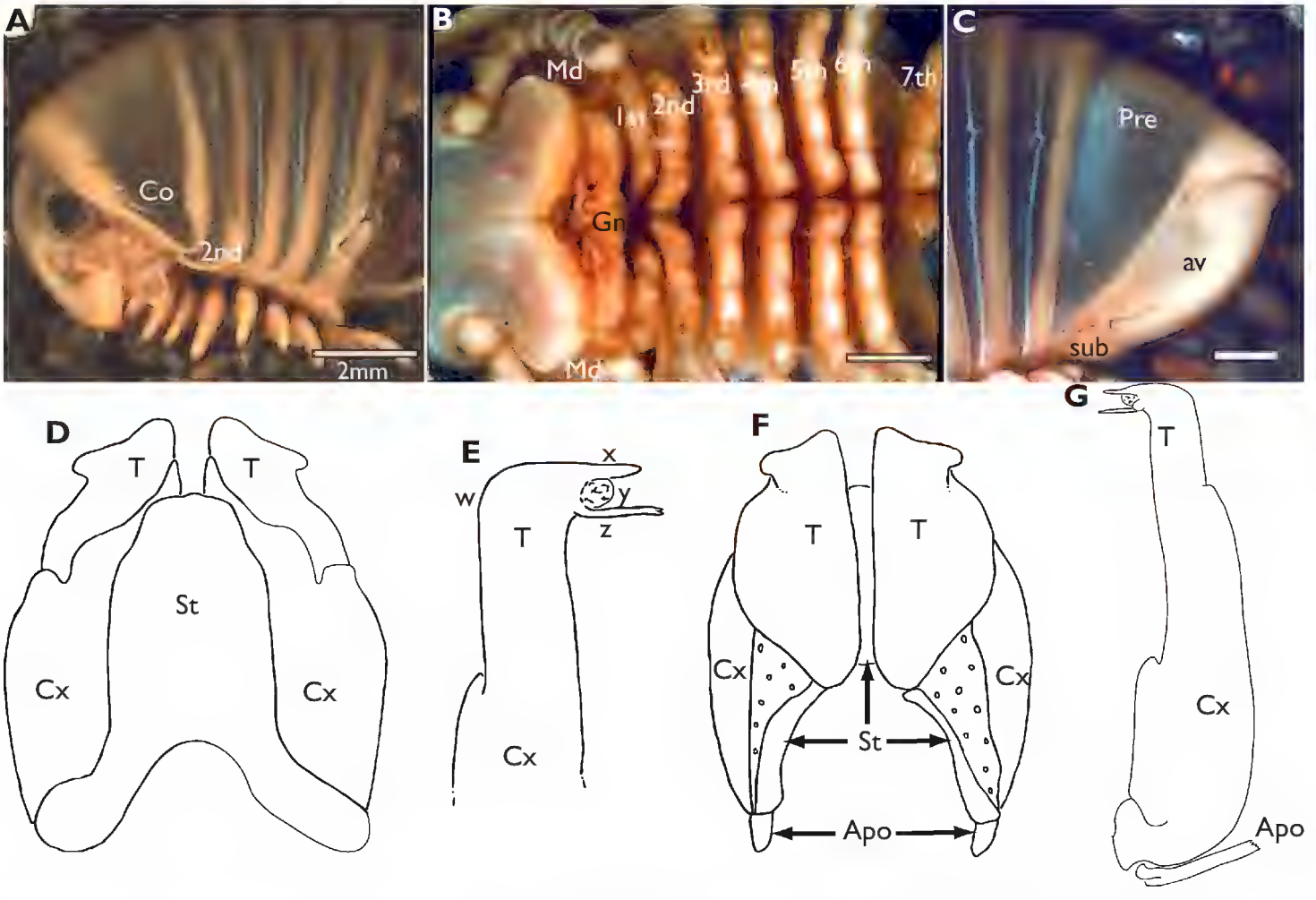

Figure 59. *Hylekobolus goodmani* sp. n., male holotype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** anterior gonopod, anterior view **E** left posterior gonopod, anterior view **F** anterior gonopod, posterior view **G** left posterior gonopod, posterior view. Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; Gn = gnathochilarium; Md = mandible; Pre = preanal ring; St = sternite; sub = subanal scale; T = telopodite. Scale bars = 1 mm.

widely projecting above telopodite margin (Fig. 59F), basally of apical process not projecting (Fig. 59F).

Posterior gonopod telopodite bent 90° (Fig. 59G). Projection absent from lateral margin (*w*, Fig. 59E). Apical process (*x*) basally extraordinary slender, only twice as wide as sperm canal (Fig. 59E). Projection of sperm canal (*z*) long and slender, running parallel to apical process (Fig. 59G). Tip sharp-edged. Membranous lobe (*y*) large and well-rounded (Fig. 59E).

Distribution and ecology: this species is only known from the Anosy Mountains, north of the Isaka-Ivondro corridor (Fig. 54).

Etymology: *goodmani*, adjective, named after Dr. Steven M. Goodman who collected this and numerous other remarkable Malagasy millipede species.

Hylekobolus montanus Wesener, sp. n.

urn:lsid:zoobank.org:act:7EE1F629-61E9-4BE1-94E8-3E10F2AE6E96

Material examined: 2 ♂, 2 ♀ *Holotype:* 1 ♂ (72 mm long), FMMC 8194, Province de Toliara, RNI Andohahela, parcel 1, 10.0 km NW Eminiminy, 1500 m, montane rainforest, 24°34.2' S, 46°43.9' E, leg. S. Goodman, 17–27.XI.1995. *Paratypes:* 1 ♀, FMMC 8194, same data as holotype; 1 ♂, 1 ♀, FMMC, Andohahela camp #5, 20 km SE Andranondambo,1875 m, montane rainforest, 24°33.7' S, 46°43.3' E, leg. S. Goodman, 27.XI.–5.XII.1995.

Differential diagnosis: see *H. goodmani* for a differentiation between both species. The posterior gonopods with the swollen, well-rounded projection (*w*, Fig. 60E) resemble closely those of *H. brachiosauroides*; see above for a separation between these two species.

Description. *Measurements*: males with 50 or 51 rings, circa 72 mm long, 5.0–5.2 mm wide. Female with 50 rings, 74 mm long, 5.8 mm wide.

Coloration: median part of collum, anterior part of telson and body rings greyish (Figs 60A, C). Head dark green. Legs and antennae reddish (Fig. 60B). Posterior margin of collum, body rings and telson light brown (Figs 60A, C). *Eyes* with 46–48 ocelli (Fig. 60A).

Anterior gonopod sternite basally wide, apically elevated into a wide, well-rounded lobe (Fig. 60D). Mesal coxite process wide and only slightly protruding (Fig. 60D). Apical process of telopodite large and well-rounded. Retrorse margin slender, widely projecting above telopodite margin (Fig. 60F); margin basally of apical process not projecting (Fig. 60F).

Posterior gonopods telopodite bent 90° (Fig. 60G). Lateral margin with a thick, swollen, well-rounded projection (*w*, Fig. 60E). Apical process (*x*) basally wide, apically tapering (Fig. 60E). Membranous lobe (*y*) large and circular (Fig. 60E). Projection of sperm canal (*z*) straight, long and slender (Fig. 60G).

Distribution and ecology: this species could until now only be collected in the Andohahela Mountains north of the Isaka-Ivondro corridor (Fig. 54), at 1500–1850 m elevation. It is currently unknown if this species is restricted to such high elevations.

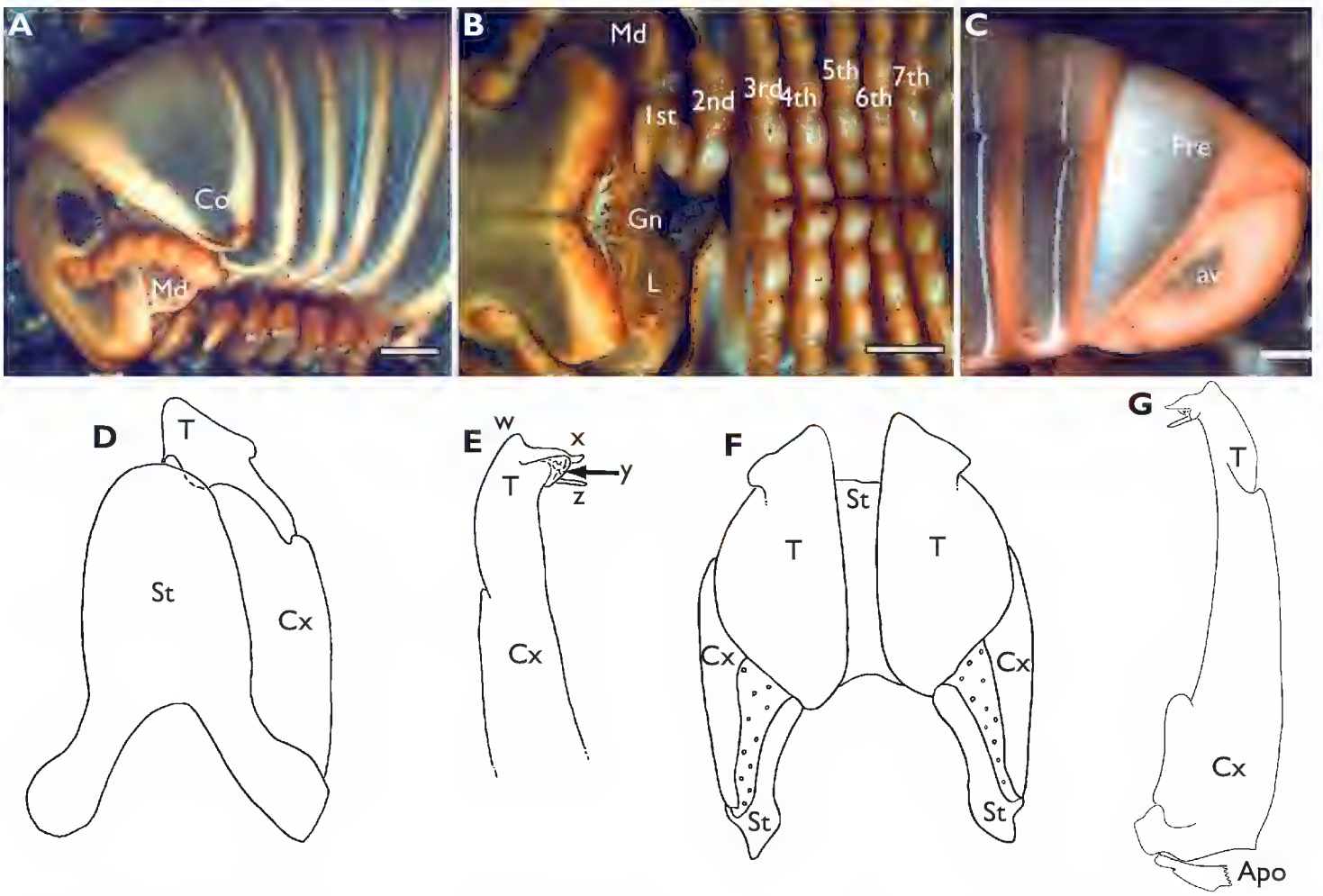

Figure 60. *Hylekobolus montanus* sp. n., male holotype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** anterior gonopod, anterior view **E** left posterior gonopod, anterior view **F** anterior gonopod, posterior view **G** left posterior gonopod, posterior view. Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; Gn = gnathochilarium; L = ledges; Md = mandible; Pre = preanal ring; St = sternite; T = telopodite. Scale bars = 1 mm.

Etymology: *montanus*, adjective, refers to the high elevation where the species was collected.

***Hylekobolus analavelona* Wesener, sp. n.**
urn:lsid:zoobank.org:act:769102C4-C297-4628-85AA-B87EEB70DF3E

Material examined: 4 ♂, 6 ♀, 3 imm. *Holotype:* 1 ♂ (56 mm long), FMMC 5429, Province Toliara, Forêt de Analavelona, near spring of Manasay River, undisturbed mid-elevation forest with dry and humid elements, 1250 m, 22°38.6' S, 44°10.3' E, leg. S. Goodman, 2–8.XI.2000, pitfall trap. *Paratypes:* 4 ♀, 2 imm., FMMC 5429, same data as holotype.

Other material examined: 3 ♂, 2 ♀, 1 imm., CAS BLF 7819 (kmp-fm-068), Province Toliara, Forêt de Analavelona, montane rainforest, 1100 m, 22°40'30" S, 44°11'24" E, leg. Griswold, Fisher et al., 18–22.XI.2003.

Differential diagnosis: *H. analavelona* has a unique green/brown colour pattern (Figs 62A, B). The colour pattern and gonopods clearly identify this species. The gonopods feature a unique combination of characters: the anterior gonopods carry a short

Figure 61. *Hylekobolus montanus* female paratype, SEM. **A** antenna, overview **B** antennomere 5 with sensilla basiconica **C** antennomere 6 with sensilla basiconica **D** gnathochilarium, part of endochilarium **E** left mandible, mesal view **F** left vulva, lateral view. 4iT = 4-combed internal teeth; av = anterior valve; cp = central pads; Endo = endochilarium; eT = external tooth; LT = lateral tooth; mp = molar plate; O = operculum; pL = pectinate lamella; pv = posterior valve; sb = sensilla basiconica.

mesal coxite process (Fig. 62D), the retrorse telopodite process is wide and projecting (Fig. 62F), the apical process (*x*) of the posterior gonopods is 4–5 times wider than the sperm canal (Fig. 62E).

Description. *Measurements*: male holotype with 45 rings, 56 mm long, 3.6 mm wide. Females with 45 rings, 49–56mm long, 4.65–5.1 mm wide.

Coloration: collum and posterior half of body rings light brown (Fig. 62A). Body rings in anterior half only laterally with dark green colour, dorsally light brown. Each

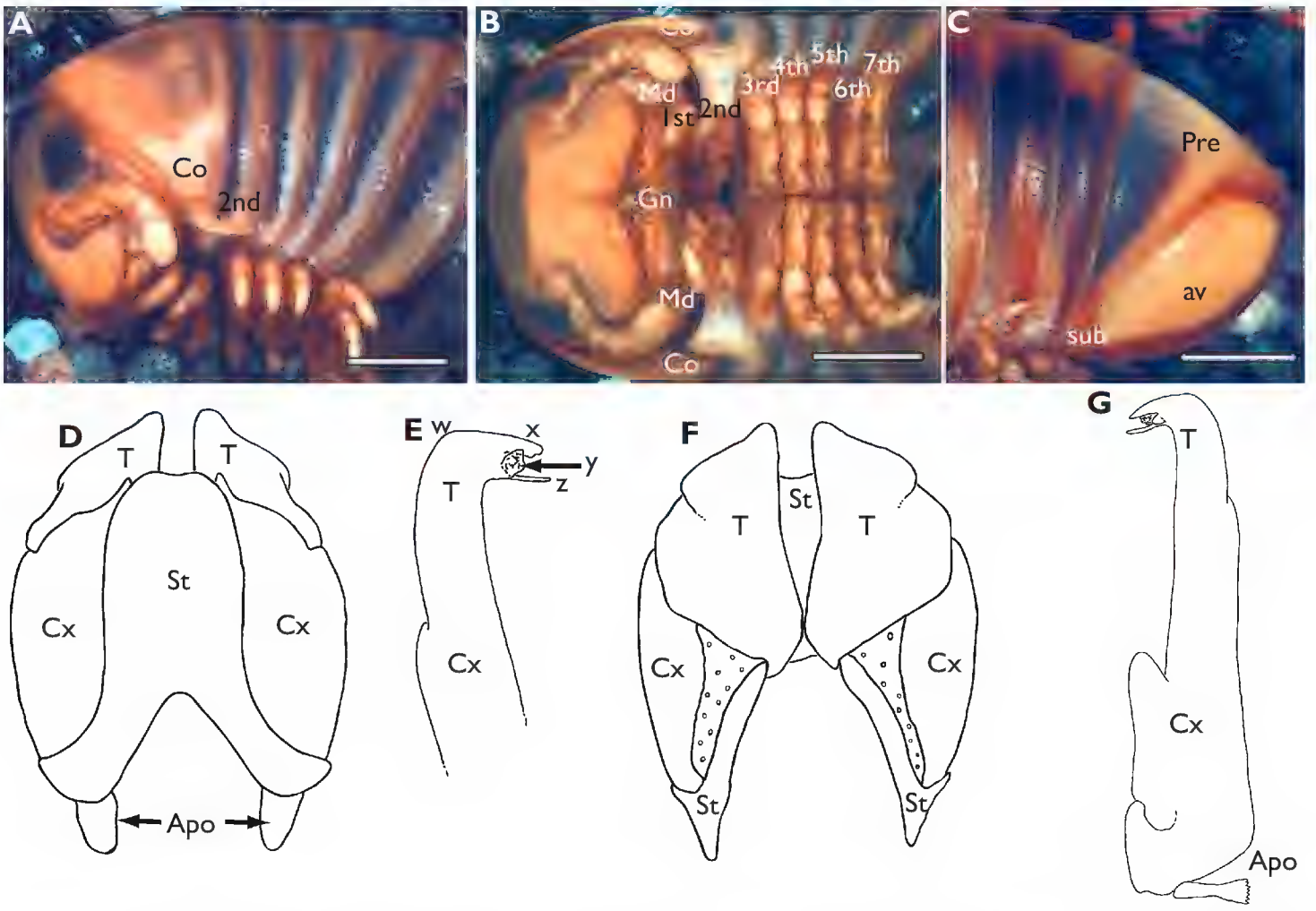

Figure 62. *Hylekobolus analavelona* sp. n., male holotype. **A** head, lateral view **B** legs 1–7, ventral view **C** telson **D** anterior gonopod, anterior view **E** left posterior gonopod, anterior view **F** anterior gonopod, posterior view **G** left posterior gonopod, posterior view. Apo = apodeme; av = anal valves; Co = collum; Cx = coxite; Gn = gnathochilarium; Md = mandible; Pre = preanal ring; St = sternite; sub = subanal scale; T = telopodite. Scale bars = 1 mm.

body ring dorsally with an isolated dark green spot. Legs and antennae light brown (Fig. 62B). *Eyes* with 32–34 ocelli (Fig. 62A).

Anterior gonopod sternite basally wide, apically elevated into a wide, well-rounded rectangular process (Fig. 62D). Mesal process of coxite wide and only slightly protruding (Fig. 62D). Apical telopodite process large and well-rounded. Retrorse margin wide, projecting above telopodite margin (Fig. 62F); margin basally of apical process not projecting (Fig. 62F).

Posterior gonopods telopodite bent 90° (Fig. 62G). Projection absent from lateral margin (*w*, Fig. 62E). Tip of apical process (*x*) sharp-edged, basally slender, 4–5 times as wide as sperm canal (Fig. 62E). Membranous lobe (*y*) large and well-rounded (Fig. 62E). Projection of sperm canal (*z*) long and slender, running parallel to apical process (Fig. 62E).

Distribution and ecology: only known from the Analavelona Mountain (Fig. 54), an isolated hilltop with rainforest in the otherwise dry southwestern region of Madagascar (DuPuy and Moat 2007).

Etymology: *analavelona*, noun in apposition, after the only place where this species can be found, the Analavelona Mountain (Fig. 54).

***Hylekobolus latifrons* Wesener, sp. n.**
urn:lsid:zoobank.org:act:4D6051E1-AC6D-4DEC-8DB9-466BB336BBB9

Material examined: 2 ♂, 1 ♀ *Holotype:* 1 ♂ (47 mm long), MNHN, Madagascar, Localité: Karianga, p. de Farafangana, alt. 700 m, région montagneuse et boisée, 22°26' S, 47°22' E, leg. Mission R. Decary, Octobre 1926, Entrée n°17–1927 *Paratypes:* 1 ♂, 1 ♀, MNHN, same data as holotype.

Differential diagnosis: the posterior gonopods of *H. latifrons* with their wide tip and additional rectangular extension (Fig. 63B), are unique.

Description. *Measurements*: males with 46 or 47 rings, circa 47 mm long, 4.1–4.2 mm wide. Female with 46 rings, 58 mm long, 4.7 mm wide.

Coloration: faded in alcohol. Anterior part of collum, posterior parts of rings, antennae, legs, anal process, valves and complete scale of lighter colour, remaining parts grey. *Eyes* with 32–34 ocelli.

Anterior gonopod sternite basally wide, apically elevated into a triangular lobe with a triangular, wide, well-rounded tip (Fig. 63A). Mesal coxite process wide and only slightly protruding (Fig. 63A). Apical process of telopodite large and well-rounded. Retrorse margin wide, projecting above telopodite (Fig. 63C); margin basally of process not projecting (Fig. 63C).

Posterior gonopods telopodite bent 90° (Fig. 63D). Telopodite 2 times longer than wide (Fig. 63B). Projection absent from lateral margin (*w*, Fig. 63B). Apical process (*x*) wide (Fig. 63B). Membranous lobe (*y*) small and well-rounded (Fig. 63B). An additional sclerotized, rectangular lobe visible in anterior view (Fig. 63B). Projection of sperm canal (*z*) long and slender, slightly curved towards apical process (Fig. 63D).

Distribution and ecology: *H. latifrons* is until now only known from old collections made 80 years ago close to Karianga, a lowland forest in Southeastern Madagascar (Fig. 54).

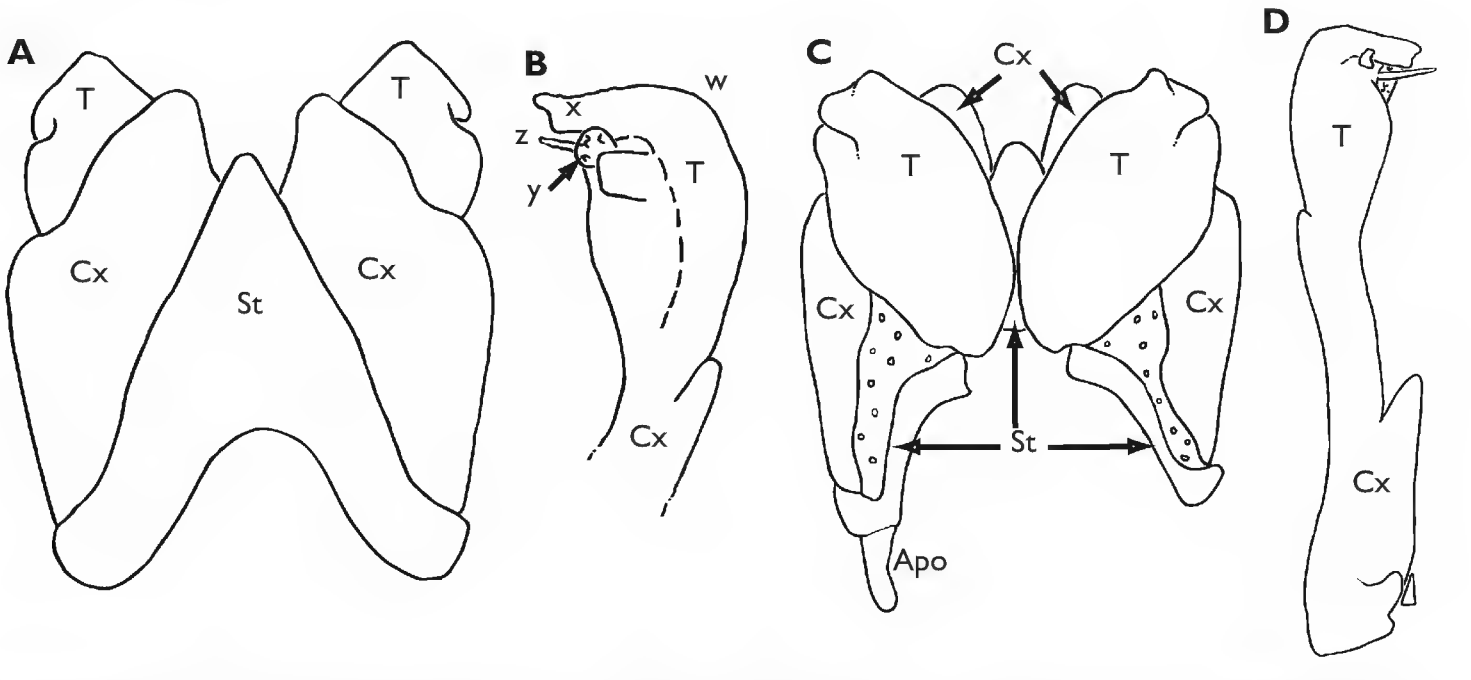

Figure 63. *Hylekobolus latifrons* sp. n., male holotype. **A** anterior gonopod, anterior view **B** right posterior gonopod, anterior view **C** anterior gonopod, posterior view; **D** right posterior gonopod, posterior view. Apo = apodeme; Cx = coxite; St = sternite; T = telopodite. Not to same scale.

Etymology: *latifrons*, noun in apposition, refers to the surprisingly wide telopodite 'face' of the posterior gonopods.

***Hylekobolus andasibensis* Wesener, sp. n.**
urn:lsid:zoobank.org:act:F84CC1D3-0775-441A-94FC-959E3799881F

Material examined: 2 ♂, 1 ♀, 2 imm. *Holotype:* 1 ♂ (42 mm long), MNHN, Madagascar, Périnet (Andasibe), rainforest, 18°55' S, 48°25' E, leg. Brygoo, III.1967, BY628. *Paratypes:* 1 ♂, 1 ♀, 2 imm., MNHN, same data as holotype.

Differential diagnosis: the posterior gonopods of *H. andasibensis* sp. n. are only curved 60°, which is unique within the genus *Hylekobolus*. The projection of the sperm canal is basally wide, apically tapering (Fig. 64D)

Description. *Measurements*: males with 47 rings, circa 42 mm long, 3.7 mm wide. Female with 47 rings, circa 63 mm long, 4.9 mm wide.

Coloration: faded to grey in alcohol. *Eyes* with circa 34 ocelli.

Anterior gonopod sternite basally wide, apically elevated into a well-rounded tip (Fig. 64A). Mesal process of coxite wide and only slightly protruding (Fig. 64A). Apical process of telopodite slender and well-rounded. Retrorse margin wide, not projecting (Fig. 64C).

Posterior gonopods telopodite bent 60° (Fig. 64D). Projection absent from lateral margin (*w*, Fig. 64B). Apical process (*x*) wide, tapering (Fig. 64B). Membranous lobe (*y*) small (Fig. 64B). Projection of sperm canal (*z*) basally wide, apically tapering, curved towards coxite (Fig. 64D).

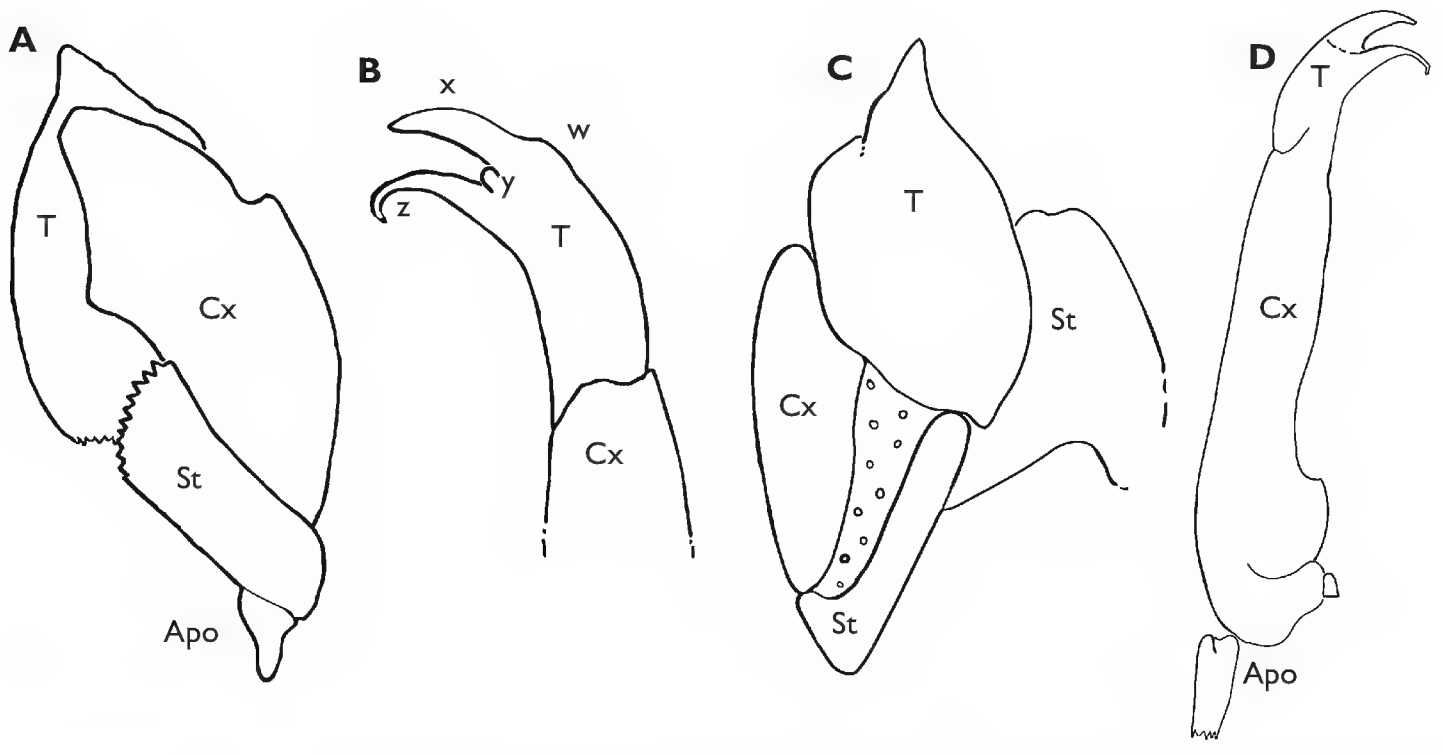

Figure 64. *Hylekobolus andasibensis* sp. n., male holotype. **A** anterior gonopod, anterior view **B** right posterior gonopod, anterior view **C** anterior gonopod, posterior view **D** right posterior gonopod, posterior view. Apo = apodeme; Cx = coxite; St = sternite; T = telopodite. Not to same scale.

Distribution and ecology: this species is only known from old collections undertaken in Andasibe, located in the central eastern half of Madagascar. *H. andasibensis* is the only known *Hylekobolus* species recorded from central Madagascar (Fig. 54).

Etymology: *andasibensis*, adjective, refers to the type locality, Andasibe.

***Hylekobolus marojejy* Wesener, sp. n.**
urn:lsid:zoobank.org:act:1A341307-5F14-4A42-8B2E-1FA759BB0020

Material examined: 2 ♂, *Holotype:* 1 ♂ (47.5 mm long), CAS BLF 9244 (CASENT 9032795), Madagascar, Province Antsiranana, Parc National de Marojejy, 25.7 km 32° NNE Andapa, 10.3 km 314° NW Manantenina, montane rainforest, 1575 m, 14°26'42" S, 049°44'30" E, leg. B. L. Fisher, 21.XI.2003 *Paratypes:* 1 ♂ (im**m.), CAS BLF 9244, sa**me data as holotype.

Differential diagnosis: the posterior gonopods of *H. marojejy* sp. n. with the large triangular expansion of the tip (x), which even carries the sperm canal (Fig. 35D), separates this species from any other *Hylekobolus* species.

Description. *Measurements*: males with 48 rings, circa 47.5 mm long, 4.4 mm wide.

Coloration: faded in alcohol. Anterior part of collum, posterior parts of rings, antennae, legs, anal process, valves and entire scale reddish, remaining parts dark grey. *Eyes* with circa 32 ocelli.

Anterior gonopod sternite basally wide, apically weakly tapering, tip well-rounded (Fig. 63A). Mesal coxite process slender and protruding (Fig. 35D). Apical process of telopodite elongated and slender. Retrorse margin wide, projecting above telopodite (Fig. 35C); margin basally of process not projecting.

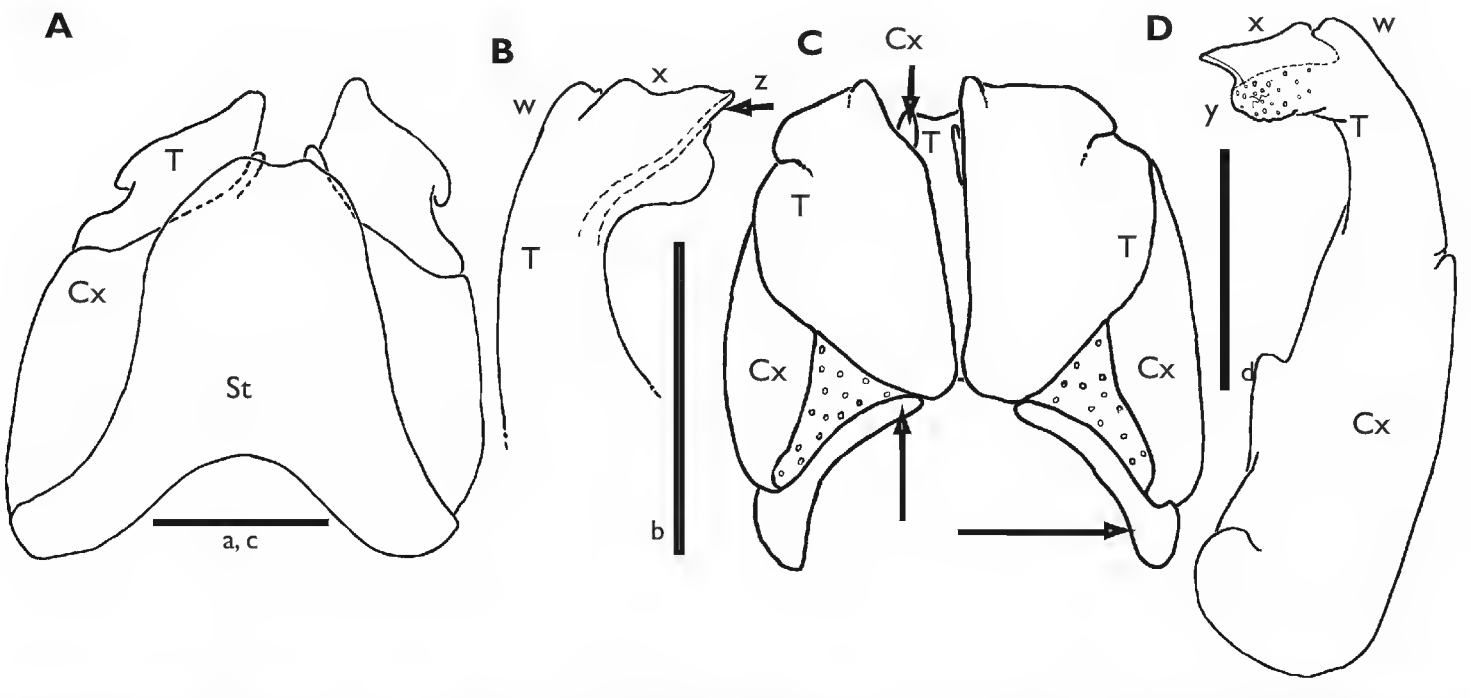

Figure 65. *Hylekobolus marojejy* sp. n., male holotype. **A** anterior gonopod, anterior view **B** right posterior gonopod, anterior view **C** anterior gonopod, posterior view **D** right posterior gonopod, posterior view. Apo = apodeme; Cx = coxite; St = sternite; T = telopodite. Not to same scale.

Posterior gonopods telopodite bent 90° (Fig. 35D). Telopodite 2 times longer than wide (Fig. 35B). Projection absent from lateral margin (*w*, Fig. 35B). Apical process (*x*) wide (Fig. 35B). Membranous lobe (*y*) small and well-rounded. An additional sclerotized, rectangular lobe visible in anterior view (Fig. 35B). Projection of sperm canal (*z*) long and slender, slightly curved towards apical process (Fig. 35D).

Distribution and ecology: *H. marojejy* sp. n. is currently only known from Marojejy (Fig. 54).

Etymology: *marojejy*, noun in apposition, refers to the type locality, the rainforest of Marojejy.

Hylekobolus anjanaharibe Wesener, sp. n.

urn:lsid:zoobank.org:act:8C8A83C0-DF66-4BAB-84A6-4EAC4B12050F

Material examined: 1 ♂, 1 ♀ *Holotype:* 1 ♂ (52 mm long), BLF CAS 8152, Madagascar, Province Toamasina, Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, montane rainforest, 1100 m, 15°10'42" S, 049°38'06" E, leg. Fisher, Griswold et al., 12–16.III.2003 *Paratype:* 1 ♀, BLF CAS 8152, same data as holotype.

Differential diagnosis: the posterior gonopods of *H. anjanaharibe* sp. n. are very wide, unique for *Hylekobolus*. The apical membranous area (*y*) is greatly enlarged, forming two large lobes (Fig. 66B).

Description. *Measurements*: male with 50 rings, circa 52 mm long, 3.8 mm wide. Female (with eggs) with 50 rings, 54 mm long, 4.2 mm wide.

Coloration: faded in alcohol. Central part of collum, anterior parts of rings, head and anal valves dark green, appendages, posterior margin of rings and preanal process light brown. *Eyes* with 32–34 ocelli.

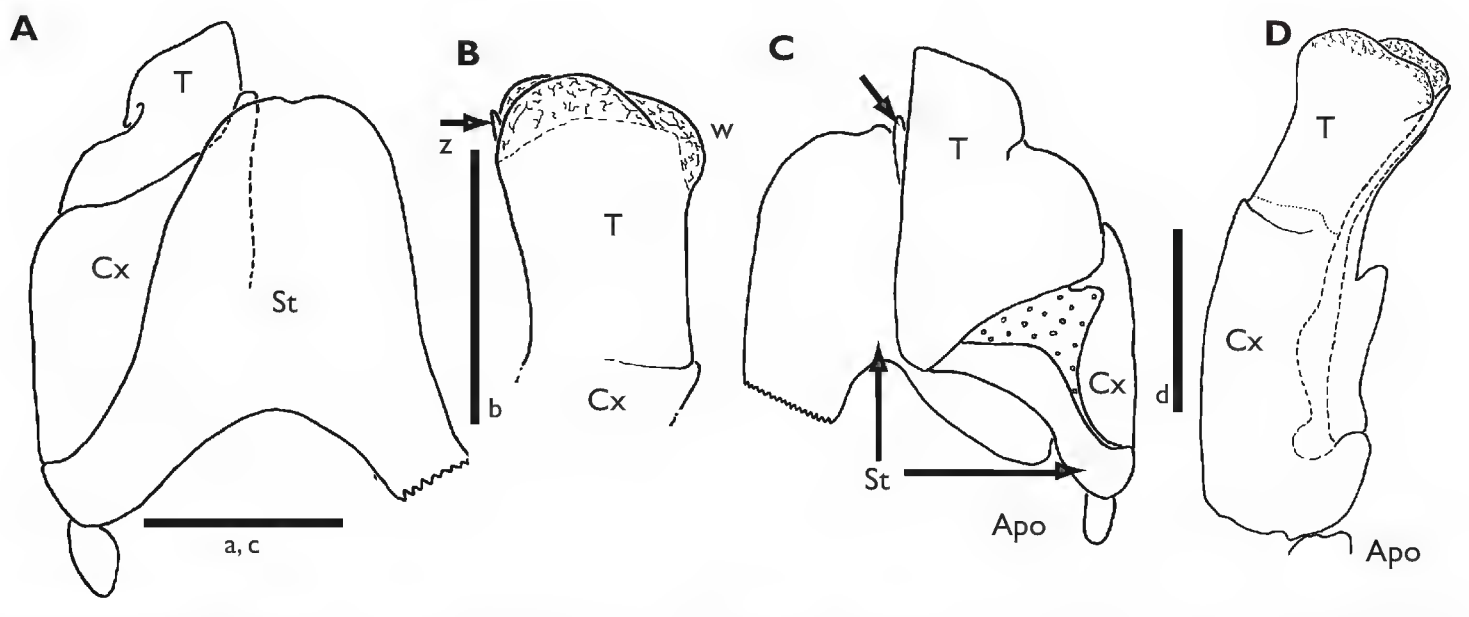

Figure 66. *Hylekobolus anjanaharibe* sp. n., male holotype. **A** anterior gonopod, anterior view **B** right posterior gonopod, anterior view **C** anterior gonopod, posterior view **D** right posterior gonopod, posterior view. Apo = apodeme; Cx = coxite; St = sternite; T = telopodite. Not to same scale.

Anterior gonopod sternite wide, with a well-rounded tip (Fig. 66A). Mesal coxite process slender and elongated (Fig. 66A). Apical process of telopodite large and well-rounded. Retrorse margin wide, slightly projecting above telopodite (Fig. 66C); margin basally of process not projecting (Fig. 66C).

Posterior gonopods telopodite always straight (Fig. 66D). telopodite of posterior gonopod only 1.5 times longer than wide (Fig. 66B). Projection absent from lateral margin (*w*, Fig. 66B), but area and tip completely covered by a whitish membranous area. Apical process (*x*) absent (Fig. 66B). Membranous lobe (*y*) bilobed, very large, covering whole tip (Fig. 66B). Projection of sperm canal (*z*) long and slender (Fig. 66D).

Distribution and ecology: *H. anjanaharibe* sp. n. is currently only known from Anjanaharibe, a mountain in north Madagascar (Fig. 54).

Etymology: *anjanaharibe*, noun in apposition, refers to the type locality, Anjanaharibe.

Nomina dubia

Four Malagasy species of Spirobolida are currently regarded as *nomina dubia*. Since their gonopods are unknown, their generic and even family position is currently unclear. The type series of two of the species could be restudied.

Rhinocricus collaris de Saussure & Zehntner, 1897

Rhinocricus collaris de Saussure & Zehntner, 1897: pl XI, fig. 45
Rhinocricus collaris, de Saussure and Zehntner 1902: 115
„Rhinocricus" collaris, Enghoff 2003: 624, lists species name

Material examined: Types: 2 ♀ (85 mm long), "types", MNHN HB015, det. H. de Saussure, "Madagascar: Grandidier". **vidi**

Observation: both female paratypes are broken and faded. The specimens are long and thick, probably reaching circa 85 mm in length and 10 mm in width, with 40 body rings. Preanal process widely protruding. Mesozonites with vertical striae, metazonites with deeply impressed longitudinal striae. The sculpturing in combination with the large body size and protruding preanal process are currently unknown from any other Spirobolida species living on Madagascar.

Comments: the strange sculpturing of the body, combined with the large size, will obviously allow to properly identify this species when new, hopefully male-containing material becomes available. The placement of *Rhinocricus collaris* in the subgenus *Rhinocricus* by de Saussure and Zehntner is probably incorrect. *R. collaris* would then be the only known member of the family Rhinocricidae ever recorded from Madagascar (Marek et al. 2003).

Spirobolus (Trigoniulus) grandidieri de Saussure & Zehntner, 1897

Spirobolus (Trigoniulus) grandidieri de Saussure & Zehntner, 1897: plate II, fig. 5.*Spirobolus (Trigoniulus) grandidieri,* de Saussure and Zehntner 1902: 141
Trigoniulus grandidieri, Enghoff 2003: 624, lists species name

Material examined: Types: 1 ♀ (60 mm long), "types", MNHN HC001, leg. Grandidier. **vidi**

Observation: colour completely faded, 50 rings, circa 60 mm long. Antennae and legs broken off. Preanal process absent.

Comments: since the type locality is unknown and the few characters available from the female type do not allow even for a family placement to be made, let alone a generic or species determination, *S. grandidieri* is regarded as a *nomen dubium*.

Spirobolus olympiacus Karsch, 1881

Spirobolus olympiacus Karsch, 1881 : 64
S. (Trigoniulus) olympiacus, de Saussure & Zehntner 1902: 129, list species name
Trigoniulus olympiacus, Enghoff 2003: 624, lists species name

Comments: the holotype is a female which was not studied. According to Karsch (1881), this species is 215 mm long, with 57 rings, and it was collected in Nosy Be, an island off northwest Madagascar. No Spirobolida species longer than 200 mm is currently known from Madagascar. Of large-bodied genera, both *Aphistogoniulus* (Wesener et al. 2009) and *Colossobolus* species (undescribed) can be found in Nosy Be.

Spirobolus (Trigoniulus) sikorae de Saussure & Zehntner, 1897

Spirobolus (Trigoniulus) sikorae de Saussure & Zehntner, 1897: plate x, fig. 35
Spirobolus (Trigoniulus) sikorae, de Saussure and Zehntner 1902: 136
Trigoniulus sikorae, Enghoff 2003: 624, lists species name

Comments: the holotype is a female which was not studied. It is not present in the MNHN collections, but may still be present at the MHNG. Since the type locality is unknown and the only known type is female, *S. sikorae* is regarded as a *nomen dubium*.

DISCUSSION

Diversity of Malagasy Spirobolida

With the descriptions presented above, there are now 62 endemic species of Malagasy Spirobolida in 15 endemic genera (Table 1). Of the two families of Spirobolida so far known from Madagascar – Pachybolidae and Spirobolellidae-- the former is now known to be represented by 14 endemic genera, compared to only seven pachybolid genera for continental Africa and seven for India (Hoffman 1980). Six of the 14 Malagasy pachybolid genera (*Madabolus* and five described here as new) are monotypic, but it is likely that more species will be added to these six genera in the future: five of the six come from eastern Malagasy rainforest whose central region is still little sampled, and more than 60% of samples examined in this study contained no mature males and were therefore not identifiable to species.

In the rainforest, up to six different genera of Spirobolida live sympatrically in the same forest-- in this case the littoral forest of Sainte Luce (Fig. 67). The diversity is lower in the dry and spiny forest, where up to three genera were collected at the same locality.

Ecology

Unlike most Malagasy giant pill-millipedes (Wesener 2009), many Spirobolida in Madagascar appear to be habitat specialists (Fig. 67). Suitable habitats for rainforest taxa of Spirobolida can be divided into five different categories:

(**1**) arboreal taxa [*Spiromimus*?, *Aphistogoniulus*],
(**2**) taxa living on or inside the first centimetres of the forest floor [*Spiromimus*?, *Caprobolus*, *Alluviobolus*, *Ostinobolus*],
(**3**) taxa only collected from deeper soil, above the root horizon [*Riotintobolus*],
(**4**) taxa only collected in or even under the root horizon [*Granitobolus*, *Ostinobolus subterraneus*],
(**5**) taxa only collected inside dead wood [*Hylekobolus*],

Most of the Malagasy rainforest species of Spirobolida, in some cases even the whole genus, are adapted to only one of the above five categories.

New character sets of potential phylogenetic importance

Some interesting morphological characters were investigated which may be of use in phylogenetic analysis in the future. For example, the molar plate of the mandible is often of a genus-specific shape. In some genera like *Caprobolus* (Fig. 40F), the molar plate is surprisingly short in comparison to other genera like *Pseudocentrobolus* (Fig. 33A). Furthermore, the expression of the transverse furrows on the molar plate can vary strongly between genera. For example, the first two furrows towards the pectinate lamella are greatly enlarged in *Hylekobolus* (Fig. 61E), while all furrows are of similar

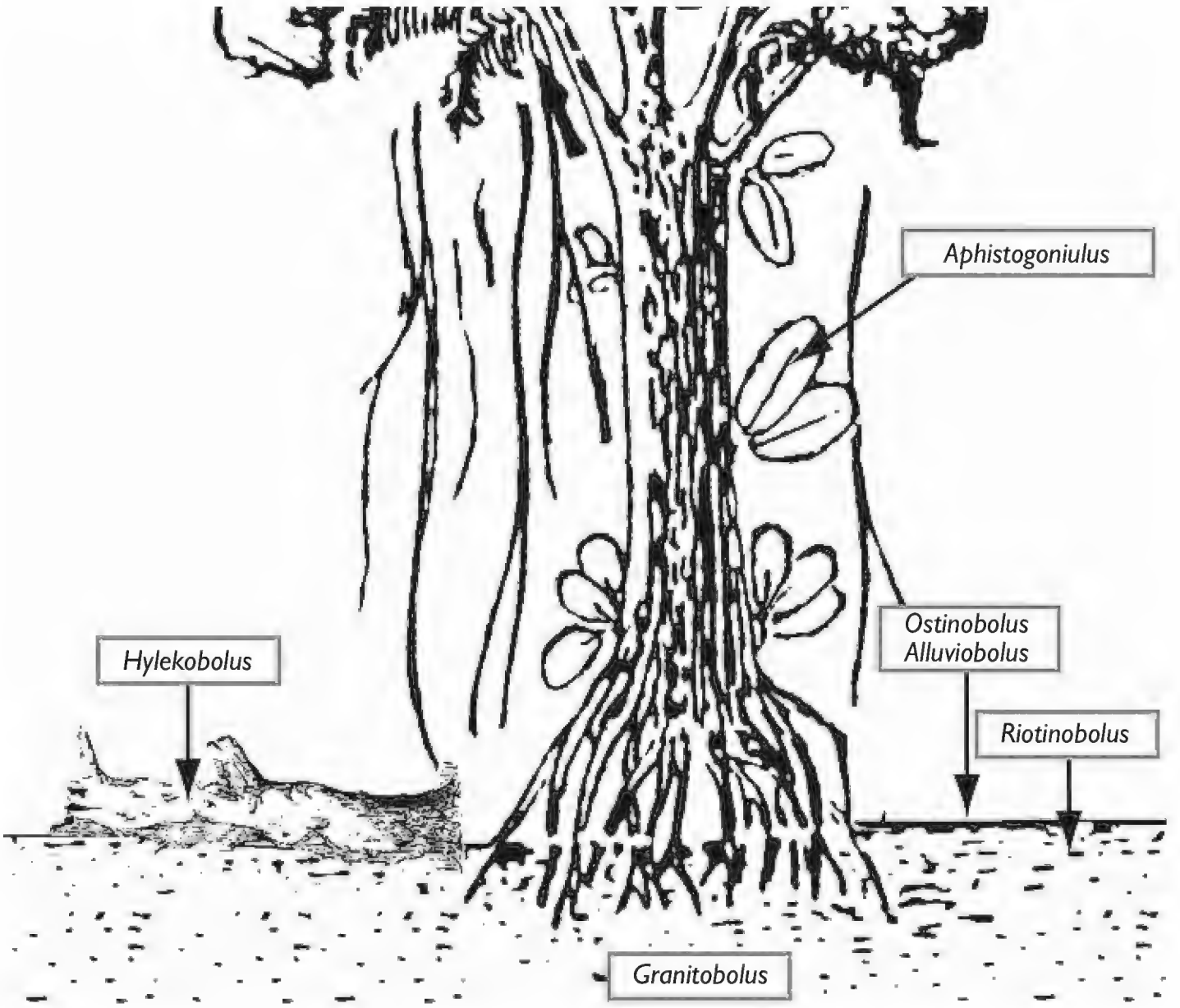

Figure 67. Schematic drawing of the littoral forest fragment S9 at Sainte Luce, with indications where six genera of Spirobolida were collected.

size in *Pseudocentrobolus* (Fig. 33A). More mandibular characters can be found in the number and shape of the mesal combed tooth. The number of combs varies between three and four even within the genus *Hylekobolus*. The extraordinary enlarged ventral tooth of *Hylekobolus* is nevertheless unique and of potential phylogenetic importance.

In six of the Malagasy genera the mentum is subdivided, a character state not reported elsewhere in Spirobolida. Scanning electron microscope studies in the future may show that this character state is more widespread.

Distribution

The two most widespread genera of Malagasy Spirobolida are also those which were described first, the large-bodied fire millipedes genus *Aphistogoniulus* Silvestri, 1897 (Wesener et al. 2009), and the tiny species of *Spiromimus* de Saussure & Zehntner, 1901 (Wesener and Enghoff, 2009). All other genera are so far only known from a single region of Madagascar. The species of *Hylekobolus* and *Ostinobolus* are restricted to humid forests. Other genera, however, are less stenoecious. Species of *Aphistogoniulus*,

Table 1. Species of Spirobolida recorded from Madagascar. Genera and species marked with an asterisk (*) are not endemic to Madagascar and were obviously introduced by humans. The nomina dubia are discussed in the result section.

Valid name	References / synonyms
SUBORDER TRIGONIULIDEA, FAMILY PACHYBOLIDAE	
Genus *Leptogoniulus* * Silvestri, 1897	
*Leptogoniulus sorornus** (Butler, 1876)	synonymy in Shelley and Lehtinen 1999
Genus *Trigoniulus* * Pocock, 1894	
*Trigoniulus corallinus** (Gervais, 1842)	synonymy in Shelley and Lehtinen 1999
Genus *Dactylobolus* *	Golovatch and Korsós, 1992
*Dactylobolus bivirgatus** (Karsch, 1881)	synonymy in VandenSpiegel and Golovatch 2007
Genus *Aphistogoniulus* Silvestri, 1897	Wesener et al. 2009
	Mystalides Attems, 1910
Aphistogoniulus cowani (Butler, 1882)	*Spirostreptus c.* Butler, 1882 *Trigoniulus sanguinemaculatus* Silvestri, 1897
Aphistogoniulus erythrocephalus (Pocock, 1893)	*Spirobolus e.* Pocock, 1893 *Mystalides quadridentatus* Attems, 1910
Aphistogoniulus hova (de Saussure & Zehntner, 1897)	*Spirobolus h.* de Saussure and Zehntner, 1897 *Spirobolus* (*Trigoniulus*) *h.* de Saussure & Zehntner 1902 *Mystalides h.* Brolemann 1922 *Aphistogoniulus polleni* Jeekel, 1971 *Aphistogoniulus brolemanni* Jeekel, 1971
Aphistogoniulus corallipes (de Saussure & Zehntner, 1902)	*Spirobolus* (*Trigoniulus*) *c.*de Saussure & Zehntner, 1902
Aphistogoniulus sakalava (de Saussure & Zehntner, 1897)	*Spirobolus s.* de Saussure & Zehntner, 1897 *Spirobolus* (*Trigoniulus*) *s.* Saussure & Zehntner 1902
Aphistogoniulus sanguineus Wesener, 2009	
Aphistogoniulus infernalis Wesener, 2009	
Aphistogoniulus diabolicus Wesener, 2009	
Aphistogoniulus aridus Wesener, 2009	
Aphistogoniulus vampyrus Wesener, 2009	
Genus *Spiromimus* de Saussure & Zehntner, 1901	Wesener & Enghoff 2009
	Pygodon de Saussure & Zehntner, 1901
Spiromimus univirgatus de Saussure & Zehntner, 1901	
Spiromimus voeltzkowi de Saussure & Zehntner, 1901	
Spiromimus dorsovittatus (de Saussure & Zehntner, 1901)	*Pygodon d.* de Saussure and Zehntner, 1901
Spiromimus triaureus Wesener & Enghoff, 2009	
Spiromimus electricus Wesener & Enghoff, 2009	
Spiromimus litoralis Wesener & Enghoff, 2009	
Spiromimus scapularis Wesener & Enghoff, 2009	

Valid name	References / synonyms
Spiromimus albipes Wesener & Enghoff, 2009	
Spiromimus laticoxalis Wesener & Enghoff, 2009	
Spiromimus simplicicoxalis Wesener & Enghoff, 2009	
Spiromimus grallator Wesener & Enghoff, 2009	
Spiromimus namoroka Wesener & Enghoff, 2009	
Spiromimus simplex Wesener & Enghoff, 2009	
Genus *Madabolus* Wesener & Enghoff, 2008	Wesener et al. 2008
Madabolus maximus Wesener & Enghoff, 2008	
Genus *Corallobolus*, gen. n.	
Corallobolus cruentus, **sp. n.**	
Genus *Sanguinobolus*, gen. n.	
Sanguinobolus maculosus, **sp. n.**	
Genus *Colossobolus*, gen. n.	
Colossobolus semicyclus, **sp. n.**	
Colossobolus oblongopedus, **sp. n.**	
Colossobolus giganteus, **sp. n.**	
Colossobolus minor, **sp. n.**	
Colossobolus litoralis, **sp. n.**	
Colossobolus aculeatus, **sp. n.**	
Colossobolus pseudoaculeatus, **sp. n.**	
Genus *Zehntnerobolus*, gen. n.	
Zehntnerobolus rubripes (de Saussure & Zehntner, 1897)	*Spirobolus r.* de Saussure & Zehntner, 1897 *Spirostrophus r.* (Saussure and Zehntner, 1897)
Genus *Flagellobolus*, gen. n.	
Flagellobolus pauliani, **sp. n.**	
Genus *Riotintobolus*, gen. n.	
Riotintobolus mandenensis, **sp. n.**	
Riotintobolus minutus, **sp. n.**	
Riotintobolus aridus, **sp. n.**	
Riotintobolus anomalus, **sp. n.**	
Genus *Pseudocentrobolus*, gen. n.	
Pseudocentrobolus aureus, **sp. n.**	
Pseudocentrobolus vohibasiensis, **sp. n.**	
Genus *Granitobolus*, gen. n.	
Granitobolus endemicus, **sp. n.**	
Granitobolus andohahelensis, **sp. n.**	
Genus *Caprobolus*, gen. n.	
Caprobolus andringitra, **sp. n.**	
Genus *Alluviobolus*, gen. n.	
Alluviobolus laticlavius, **sp. n.**	
Alluviobolus tsimelahy, **sp. n.**	
Alluviobolus antanosy, **sp. n.**	
Genus *Ostinobolus*, gen. n.	
Ostinobolus rufus, **sp. n.**	

Valid name	References / synonyms
Ostinobolus stellaris, **sp. n.**	
Ostinobolus montanus, **sp. n.**	
Ostinobolus subterranus, **sp. n.**	
SUBORDER SPIROBOLIDEA, FAMILY SPIROBOLELLIDAE	
Genus *Hylekobolus*, gen. n.	
Hylekobolus brachiosauroides, **sp. n.**	
Hylekobolus rufus, **sp. n.**	
Hylekobolus griseus, **sp. n.**	
Hylekobolus albicollaris, **sp. n.**	
Hylekobolus goodmani, **sp. n.**	
Hylekobolus montanus, **sp. n.**	
Hylekobolus analavelona, **sp. n.**	
Hylekobolus latifrons, **sp. n.**	
Hylekobolus andasibensis, **sp. n.**	
Hylekobolus marojejy, **sp. n.**	
Hylekobolus anjanaharibe, **sp. n.**	
NOMINA DUBIA	
Rhinocricus collaris de Saussure & Zehntner, 1897	
Spirobolus (*Trigoniulus*) *grandidieri* de Saussure & Zehntner, 1897	*Trigoniulus g.* (de Saussure & Zehntner, 1897)
Spirobolus olympiaceus Karsch, 1881	*Trigoniulus g.* (Karsch, 1881)
Spirobolus (*Trigoniulus*) *sikorae* de Saussure & Zehntner, 1897	*Trigoniulus s.*(de Saussure & Zehntner, 1897)

Spiromimus, *Colossobolus* and *Riotintobolus* live in rainforests as well as in dry and spiny woodlands. This broad ecological capacity, however, is not reflected at the species level within these genera. Not a single Malagasy species of Spirobolida has been collected in dry and humid forests simultaneously.

Conservation

Of special interest from a conservation point of view are microendemic species which were only collected in single, highly endangered forests-- namely the isolated Western rainforest of the Analavelona Mountain, the littoral subhumid forest of Petriky, the littoral rainforest of Mandena and tiny rainforest remnants on the isolated Ambatotsirongorongo Mountain.

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